Académie de Paris

Université Pierre et Marie Curie
Thèse de doctorat

Spécialité : Ecohydrologie
Ecole Doctorale "Diversité du Vivant"

Présentée par
Séraphine Grellier

Pour obtenir le grade de
DOCTEUR de l'UNIVERSITÉ PIERRE ET MARIE CURIE

Invasion ligneuse par l'*Acacia sieberiana* dans un pâturage raviné du KwaZulu-Natal (Afrique du Sud)

Soutenue publiquement le 27 juin 2011

Devant le jury composé de :

Pr. Luc Abbadie	Directeur de recherche CNRS	Directeur de thèse
Dr. Christian Valentin	Directeur de recherche IRD	Co-directeur de thèse
Dr. Bernard Riéra	Chargé de recherche CNRS MNHN	Examinateur
Pr. Jean-Yves Dubuisson	Professeur à l'UPMC	Examinateur
Pr. Simon Lorentz	Professeur à l'Université du KwaZulu-Natal	Examinateur
Dr. Luc Descroix	Chargé de recherche IRD	Rapporteur
Pr. Thierry Dutoit	Professeur à l'Université d'Avignon	Rapporteur

Laboratoire de Biogéochimie et écologie des milieux continentaux
(UMR 7618)
Ecole Normale Supérieure,
46 Rue d’Ulm, 75230 Paris Cedex 05

Institut de Recherche pour le Développement (IRD)
IRD c/o Bioresources Engineering and Environmental Hydrology (BEEH)
Université du KwaZulu-Natal,
Rabie Saunders building,
Private bag X01, 3209 Scottsville, Afrique du Sud

Université Pierre & Marie Curie - Paris 6
Bureau d’accueil, inscription des doctorants et base de données
Esc G, 2ème étage
15 rue de l’école de médecine
75270-PARIS CEDEX 06

Tél. Secrétariat : 01 42 34 68 35
Fax : 01 42 34 68 40
Tél. pour les étudiants de A à EL : 01 42 34 69 54
Tél. pour les étudiants de EM à MON : 01 42 34 68 41
Tél. pour les étudiants de MOO à Z : 01 42 34 68 51
E-mail : scolarite.doctorat@upmc.fr

Remerciements

Ce travail est l'aboutissement de plusieurs années en Afrique du Sud. La réalisation de ce projet a été possible grâce à toutes les personnes que j'ai rencontrées, et avec qui j'ai partagé un peu ou beaucoup de mon temps au cours de ces quatre années. L'investissement personnel au cours d'une thèse n'est plus à démontrer, et parmi toutes ces personnes, qui sont nombreuses, beaucoup sont bien plus que des collègues. J'ai envie de les remercier toutes pour ce qu'elles sont et ce qu'elles ont pu m'apporter ainsi qu'à ces travaux.

Tout à commencé par l'envoi d'une lettre de motivation il y a six ans pour un stage à l'étranger dans la recherche. C'est à Christian Valentin que je dois la réception bienveillante de cette lettre et le début d'une longue histoire. Christian est aujourd'hui co-directeur de ma thèse : merci Christian pour ce que *vous* avez rendu possible professionnellement et personnellement!

Je tiens à exprimer ma gratitude envers Luc Abbadie qui a accepté d'être mon directeur de thèse, ainsi qu'envers de nombreux collègues-encadrants qui ont contribué à ce travail : Sébastien Barot, Nicolas Florsch, Jean-Louis Janeau, Simon Lorentz, Pascal Podwojewski, David Ward. Chacun d'entre eux, de France ou d'Afrique du Sud a été d'une grande aide, de très bons conseils et d'un soutien inestimable et inlassable tout au long de cette thèse : merci à vous tous, thanks to all of you.

Merci aux membres du jury d'avoir accepté de participer et surtout de s'être rendus disponibles pour cette thèse.

Je remercie également les deux laboratoires au sein desquels j'ai effectué cette thèse : Bioemco et le *Bioresources Engineering and Environmental Hydrology* (BEEH) en Afrique du Sud. C'est donc tous les collègues de ces deux laboratoires que je remercie chaleureusement et notamment Graham Jewitt et Jeff Smithers pour leur accueil durant trois années au sein du BEEH. Merci à l'Institut de Recherche pour le Développement (IRD) et au projet SAFEWater de la fondation nationale de recherche sud africaine (NRF), administré par la « Water Research Commission », pour le financement de ce projet.

Le laboratoire de Grignon m'a également accueilli pendant un mois et je remercie donc sincèrement Thierry Bariac et Patricia Richard pour leur soutien et les longues heures passées à distiller des sols.

Le laboratoire « *Biological and Conservation Sciences* » de l'Université du KwaZulu-Natal (UKZN) à travers David Ward m'a permis de réaliser de nombreux travaux et je remercie aussi tous les collègues et étudiants de ce laboratoire.

Sans la communauté de Potshini et Joe Culverwell, évidemment, rien n'aurai été possible sur le terrain. J'envoie donc un grand merci à l'ensemble de la communauté et à Joe pour leur compréhension et leur participation, et plus particulièrement à Sibonelo Mabaso et toute sa famille.

Je voudrais remercier simplement et du fond du cœur tous ceux qui ont été présents et qui ont participé, ne serait-ce que quelques heures à l'aboutissement de cette thèse :

- Mes amis qui ont expérimenté les griffures d'acacias et qui ont participé avec le sourire à des expérimentations pas toujours faciles durant leurs vacances : Frederick Cooper, Denis Gourdon, Lucie Tiercelin-Parent, Edouard Parent, Francois-Xavier Parent.
- Un ami cher, Pierre Gerin, qui m'a hébergée et bichonnée par ses petits plats lors de mes passages sur Paris : merci Pierre.
- Les étudiants et post-doc français, sud-africain, swazis ou autre, dont certains sont aussi devenus des amis : Simon Besnard, Olivier Bonnet, Dalton, Pheshaya Dlamini, Pauline Ferry, Moses Gichua, Ivan Janeau, Lucas Janeau, Sabrina Juarez, Charmaine Nontokozo-Mshunu, Ernest Oakes, Goncha Okay, Desale Okubamichael, Craig Orchard, Magali Proffit, Sylvain Revil-Baudard, Jean Schuermans, Andile Shange, Sindy, Neeta Soni, Gary Stafford, Mathieu Texier, Thandeka et Kyle Tomlinson. Merci à tous.
- Tous les chercheurs avec qui une collaboration a été possible toujours dans la bonne humeur : Katrin Meyer, Kerstin Wiegand et leurs collègues de l'université de Göttingen ; Jean Asseline, Shaun Berry, Patrice Cadet, Christian Camerlynck, Jean-Marie Fritsch, Jaco Kemp, Muriel Llubes, Edith Perrier, Jean-Louis Rajot, Myriam Schmutz.
- Les habitants de Potshini qui ont fait un travail remarquable sur le terrain que mes petit bras « yaourt » ne pouvaient surmonter seuls : Delane, John, Monje, Reginald, Senzo, Sibonelo, Thabane, Zanele et tous ceux dont je n'ai pu retenir le nom.
- Notre logeuse à Bergville qui est devenue une mamie adoptive : Carol Irish.
- Les collègues et personnels de l'UKZN et en particulier Debby Davy, Tad Dorasamy, Terry Everson, Martin Hampton, Alan Hill, Ignatuis, Kevin Kirkman, Ernest Kunene, Suzane Kunz, Jerry Naiken, John Ngeleka, Christina Potgieter, Cobus Pretorius, Sam, Sabine Stuart-Hill, Vanessa Stuart et Stephany, Sean Thornton-Dibb, Alison Young, Peter Zacharias et Zondy.
- Je n'oublie pas toutes les rencontres extraordinaires et amitiés en Afrique du Sud et au Vietnam en dehors du cadre de ma thèse dont certaines m'ont beaucoup marquées et resteront intensément ancrées dans ma mémoire. Je n'oublie pas non plus mes amis en France ou ailleurs, toujours présents malgré la distance : merci !

Ces remerciements s'achèvent par le meilleur et l'indispensable : ma famille, toujours aussi présente, encourageante, et compréhensive (merci Dom pour ta relecture finale), ainsi que l'homme qui partage ma vie, Jean-Louis. Notre histoire d'amour extraordinaire a rendu possible tout cela. Je lui dédie donc ces travaux.

Mots clés : *Acacia sieberiana*, Afrique du Sud, érosion, invasion ligneuse, ravine

Résumé

La dégradation des pâturages dans le monde entier s'intensifie avec l'augmentation des populations humaines. L'invasion d'espèces ligneuses endémiques et l'érosion en ravine affectent les prairies naturelles et les savanes. Les mécanismes de contrôle et les conséquences de l'invasion ligneuse sur les écosystèmes sont toujours au cœur d'un débat scientifique. Cette étude a pour but de caractériser l'invasion ligneuse au sein de pâturages ravinés. Elle apporte des réponses sur les interactions entre les principaux facteurs de contrôle et sur les conséquences de l'invasion sur l'érosion en ravine et les propriétés du couvert herbacé et du sol en prenant pour exemple un pâturage raviné du KwaZulu-Natal en Afrique du Sud envahi par l'*Acacia sieberiana.*

L'analyse de photographies aériennes a montré la transformation de cette prairie en savane en 35 ans. La population d'*A. sieberiana* présente une répartition spatiale hétérogène et privilégie les zones de plus faible teneur en argile du sol. La compétition entre la strate herbacée et les plantules d'*A. sieberiana* est le mécanisme principal limitant la survie des plantules. Le feu et l'herbivorie, en diminuant le couvert herbacé, ont un effet indirect positif sur la survie des plantules. Les acacias, en fonction de leur taille, adaptent la profondeur de prélèvement de l'eau au cours des saisons favorisant leur persistance.

Malgré leurs effets positifs sur la strate herbacée et les sols, les acacias augmentent l'érosion en ravine dominée par des processus de subsurface et favorisent la présence d'une astéracée, *Senecio inaequidens,* toxique pour les vaches. Une gestion spatiale de l'invasion est proposée pour ces pâturages ravinés.

Title: Hillslope encroachment by *Acacia sieberiana* in a deep-gullied grassland of KwaZulu-Natal (South Africa)

Keywords: *Acacia sieberiana*, encroachment, erosion, grassland, gully, South Africa

Abstract

Degradation of grasslands worldwide is intensifying due to human population increase. Tree encroachment and soil erosion are some of the major issues to be tackled in grasslands. Despite the extent of tree encroachment, its mechanisms and effects on the ecosystem are still actively debated. This study focuses on tree encroachment in grassland affected by gully erosion. The main goals are to highlight the interactions of the main factors controlling encroachment and their consequences for gully erosion and grass and soil properties. The study was undertaken in a grassland of KwaZulu-Natal (South Africa) where encroachment by *Acacia sieberiana* and deep natural gullies are observed.

Aerial photographs confirmed the transformation of the grassland into savanna within 35 years. Soil properties constitute one of the causes of the spatial distribution of *A. sieberiana* population in this grassland. Adult trees are located mainly in areas with lower clay content. Competition between grass and young *A. sieberiana* seedlings is the main process limiting survival of tree seedlings in the grassland. Fire and herbivory had a strong positive indirect effect on tree seedlings by decreasing grass cover. These trees alter their water uptake depth between seasons which may favor their survival.

Despite their positive effects on grass and soil properties, trees increased gully erosion mainly dominated by subsurface processes, and trees facilitated the growth of *Senecio inaequidens* (Asteraceae) which is toxic for cattle. Management of encroachment is proposed: trees should be kept in gullies where they maintain soil and promote grass growth, but trees should be controlled upstream gully heads.

Table des matières

Introduction : les pâturages, un écosystème fragile soumis à de fortes pressions

Pâturage du piedmont du massif du Drakensberg au KwaZulu-Natal (Afrique du Sud) envahi par *Acacia sieberiana* et fortement érodé.

Les écosystèmes pastoraux sont en permanente évolution en réponse à des modifications d'origines naturelles et anthropiques de l'environnement. Dans le contexte actuel de changement climatique global et d'augmentation de la population, les pâturages sont très sollicités et soumis à de fortes pressions. Les changements de végétation au sein de ces écosystèmes sont de plus en plus fréquents (Ojima *et al.* 1994) et leur dégradation s'accélère.

Les pâturages, espaces réservés ou dédiés à la pâture d'animaux sauvages ou d'élevage, occupent près de 40 % de la surface totale des terres dans le monde (Asner *et al.* 2004, World Resources Institute). Environ 40 % de la population mondiale dépend directement de ces terres (Reynolds *et al.* 2007). L'invasion par des arbres est une expression de leur évolution et ce phénomène touche les pâturages naturels dans le monde entier. Certains pays, comme l'Afrique du Sud, sont très sensibilisés vu l'ampleur du phénomène dans ce pays (Tainton 1999).

L'invasion d'arbres ou invasion ligneuse est définie par l'augmentation de la densité d'arbres. Le terme équivalent en anglais est « *encroachment* » à différencier de « *invasion* » qui considère des espèces invasives « aliens », ce qui constitue une autre problématique. C'est donc le terme francais d'invasion qui sera utilisé par la suite dans ce mémoire au sens de « *encroachment* » qui désigne une forte augmentation de la densité d'arbres d'espèces endémiques (Van Auken 2009). Ce phénomène touche les pâturages naturels, des climats arides (Wiegand *et al.* 2005) aux climats plus humides (Briggs *et al.* 2005, Gignoux *et al.* 2009), chauds ou froids sans distinction, mais opérant selon différents mécanismes (Archer *et al.* 1995, Scholes et Archer 1997, House *et al.* 2003, Sankaran *et al.* 2004, 2005, Ward *et al.* 2005) et pouvant avoir d'importantes conséquences positives ou négatives sur les écosystèmes (Archer *et al.* 2001, Treydte *et al.* 2007, Ludwig *et al.* 2008, Knaap *et al.* 2008, Graz 2008, Van Auken 2009). Le phénomène d'invasion ligneuse a été mise en évidence il y a près de 150 ans (Van Auken 2009) indépendamment des successions végétales durant les périodes de glaciation et inter-glaciation. Depuis le $19^{\text{ième}}$ siècle, qu'il s'agisse de prairies naturelles dominées principalement par un couvert herbacé ou de savanes (prairies tropicales) dans lesquelles arbres et herbes cohabitent, les équilibres écologiques peuvent être rompus favorisant le développement de la strate arborée. On peut alors considérer ce système « arbre-herbe » dans un continuum évoluant entre une prairie (dominée par les herbacées), une savane et même une zone boisée (House *et al.* 2003).

L'érosion hydrique est un autre phénomène important qui affecte ces écosystèmes fragilisés. Qu'elles soient d'origines anthropiques ou naturelles, tant l'érosion en nappe que l'érosion en ravine (ou « érosion linéaire ») peuvent affecter les pâturages (Poesen *et al.* 2003). Les pertes en sol liées à ces types d'érosion réduisent la qualité et la surface des pâturages qui induisent à la fois des conséquences écologiques et économiques (Bull 1981, Lal, 1998, Descroix *et al.* 2001, Poesen *et al.* 2003, Valentin *et al.* 2005). L'impact du couvert végétal sur l'érosion hydrique, déjà bien établi (Vandekerckhove *et al.* 2000, Ward *et al.* 2001, Podwojewski *et al.* sous presse), suggère de possibles interactions avec l'invasion ligneuse (Martin et Morton 1993, Petersen et Stringham 2008, Muñoz-Robles *et al.* 2010). Ce travail porte essentiellement sur l'érosion en ravine qui représente les pertes en sol les plus importantes (Valentin *et al.* 2005) et touche de nombreux paysages de par le monde, notamment les pâturages du KwaZulu-Natal en Afrique du Sud (Hoffman et Ashwell 2001, Le Roux *et al.* 2007). Les processus opérant dans les pâturages, qu'il s'agisse de l'invasion ligneuse ou de l'érosion en ravine, sont intrinsèquement liés et participent à l'évolution et aux changements observés dans ces écosystèmes. Les paragraphes suivants constituent ainsi une synthèse bibliographique des facteurs régissant l'invasion ligneuse dans les pâturages et ses conséquences sur ce type d'écosystème raviné.

I. Les facteurs et mécanismes de contrôle de l'invasion ligneuse

Les mécanismes contrôlant l'invasion par les arbres régissent en fait les équilibres « arbre-herbe » et ont fait et font toujours l'objet de nombreuses études en raison de la complexité des interactions et du large spectre des climats, des types de sol, des espèces herbacées et espèces ligneuses mis en jeu (Archer *et al.* 1995; Jeltsch *et al.* 1996, Higgins *et al.* 2000; House *et al.* 2003, Sankaran *et al.* 2004, 2005, Ward 2005, Briggs *et al.* 2005, Kraaij et Ward 2006, Wiegand *et al.* 2006, Meyer *et al.* 2007, Britz et Ward 2007, Bond 2008, Wigley *et al.* 2009, Gignoux *et al.* 2009). Les changements climatiques (températures, précipitations, augmentation du dioxyde de carbone dans l'atmosphère), une herbivorie chronique, la fréquence des feux, une modification de la compétitivité de la strate herbacée, la dissémination des graines par le bétail, l'impact de certains petits mammifères sur les graines d'arbres, et une combinaison de l'ensemble de ces facteurs ont été évoqués comme pouvant être les causes de l'invasion ligneuse (Van Auken *et al.* 2009). Un consensus ressort cependant des nombreuses études sur l'identification des facteurs principaux de l'invasion mettant en avant l'eau, les nutriments, le feu et l'herbivorie (Sankaran *et al.* 2004, Kraaij et Ward 2006). En effet, si l'impact de l'augmentation du dioxyde de carbone dans l'atmosphère peut favoriser les plantes ayant un mécanisme de transformation du CO2 atmosphérique en C_3 (Ehleringer 2005, Ward 2010), c'est-à-dire globalement les ligneux, ces derniers pourraient donc être favorisés par rapport à une strate herbacée présentant des caractéristiques de plante en C_4. Seulement, de nombreux pâturages, d'altitude notamment, sont constitués de strates arborées en C_3 et de strates herbacées également en C_3, et sont aussi affectés par l'invasion ligneuse.

Les systèmes « arbre-herbe » sont des systèmes dynamiques dans lesquels les différents facteurs de contrôle (principaux ou secondaires) sont en interaction continue dans l'espace et le temps. On peut les résumer avec une représentation schématique du système (Fig. 1).

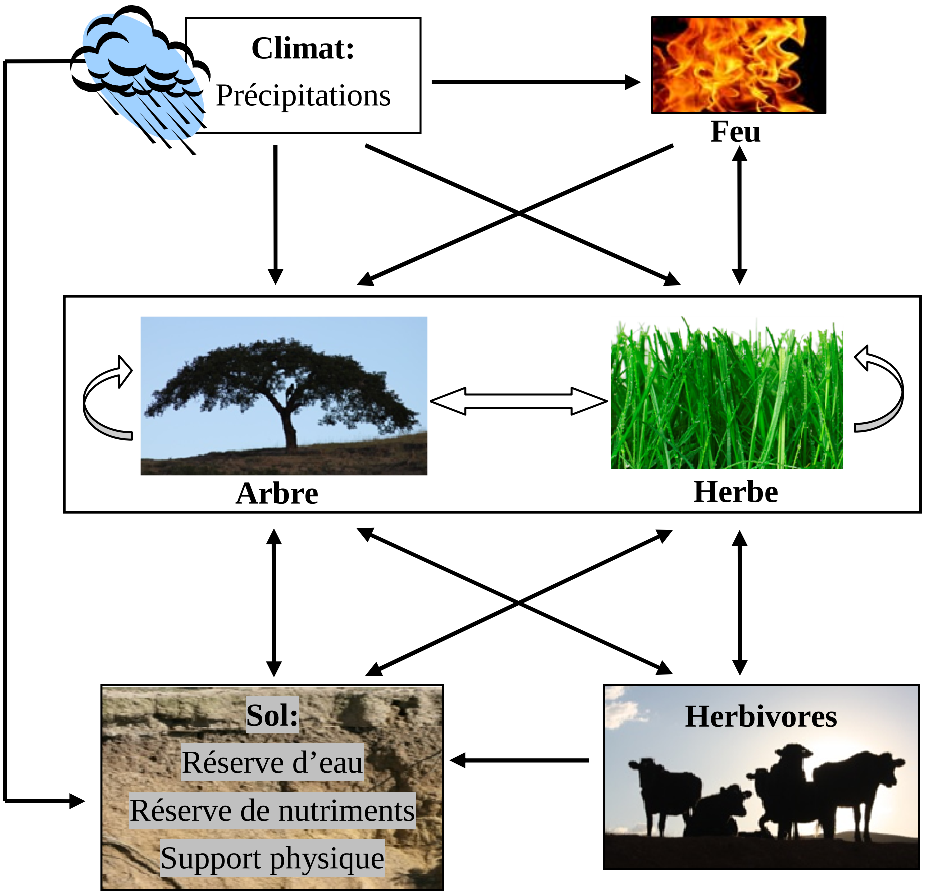


Figure 1. Principaux facteurs de contrôle de l'invasion ligneuse dans les pâturages et conséquences sur l'écosystème. Le facteur anthropique agit à un niveau non représenté ici sur le feu, les arbres, les sols et les herbivores.

Les sols : en tant que support physique, réserve d'eau et de nutriments, les sols constituent un des éléments majeurs du système pour le développement d'un couvert herbacé et arboré.

Le climat : les précipitations, qui rechargent les sols en eau, sont un des facteurs nécessaires à la germination (Kraaij et Ward 2006), à la croissance et au développement des espèces ligneuses et herbacées. Dans certaines conditions (un excès d'eau en général), les précipitations peuvent accélérer l'érosion hydrique des sols (Yaalon 1987, Poesen *et al.* 2003, Bouchnak *et al.* 2009, Samani *et al.* 2010), et limiter les feux.

Le couvert herbacé : il peut être en compétition directe avec les arbres, notamment les jeunes plantules pour la ressource en eau, les nutriments et la lumière (Wilson 1988, Kraaij et Ward 2006, Cramer *et al.* 2007). Il peut limiter la croissance des jeunes arbres et même des arbres adultes (Simmons *et al.* 2007, Riginos 2009a). Le couvert herbacé, en tant que carburant, est un élément régulateur de l'intensité et de la fréquence des feux (Van Auken 2009). Il est aussi un élément permettant la présence des herbivores sur les pâturages. Il joue un rôle positif sur les sols. L'interception des pluies par les parties aériennes limite la formation de croûtes de surface et favorise l'infiltration de l'eau dans le sol (Casenave et Valentin 1992, Neave et Rayburg 2007, Podwojewski *et al.* 2011). Son mat racinaire favorise la stabilité du sol (Gyssels et Poesen 2003). Ces deux mécanismes sont importants pour la limitation de l'érosion hydrique. Le couvert herbacé rentre aussi dans le cycle des nutriments du sol lors de sa décomposition ou lorsqu'il est brûlé (apport de potasse au sol).

Le feu : en fonction de son intensité et de la date à laquelle le feu est réalisé, il détruit les jeunes pousses d'arbres (Trollope 1980, Roques *et al.* 2001) et limite l'invasion dans de nombreux pâturages (Fuhlendorf *et al.* 2008). Les feux réduisent le couvert herbacé (Mbatha et Ward 2010) et peuvent donc indirectement limiter l'invasion ligneuse. A des fréquences modérées, c'est un facteur prépondérant dans l'entretien du pâturage et indispensable dans certains milieux (Bond et Keeley 2005, Van Auken 2009).

Les herbivores : les herbivores et plus spécifiquement les paisseurs (*grazers*) ont une forte influence sur le couvert herbacé (Mbatha et Ward 2010, Goheen *et al.* 2010) en réduisant sa biomasse. Si leur action demeure modérée, elle peut, dans certain cas, permettre le maintien d'une herbe de bonne qualité (Bonnet *et al.* 2010). Les brouteurs (*browsers*) ont un impact généralement négatif sur les arbres (Fornara et du Toit 2008, Sankaran *et al.* 2008). L'action des herbivores sur le sol peut être positive par apport direct au sol de matière organique contenu dans les bouses. La présence de bousiers associés aux bouses pourra alors augmenter la porosité du sol et favoriser l'infiltration de l'eau dans le sol (Brown *et al.* 2010). Cependant, les herbivores ont aussi un effet négatif sur les sols par compaction et par le piétinement et la création de chemins d'animaux qui sont souvent à l'origine d'érosion en ravine (Valentin *et al.* 2005).

Les arbres : ils limitent ou facilitent eux-mêmes leur propre dynamique par une compétition ou une facilitation pour les ressources. Le bilan de ces rétroactions peut dans certains cas évoluer entre facilitation et compétition en fonction du stade considéré (Callaway et Walker 1997, Miriti 2006, Kambatuku *et al.* sous presse).

Le facteur anthropique : l'homme, présent dans cet écosystème agit sur la population d'arbres directement par coupe pour une utilisation domestique (chauffage, cuisson des aliments) ou thérapeutique (remèdes confectionnés à partir de certaines espèces ligneuses culturellement importantes). Il gère les troupeaux d'élevage et donc la charge d'animaux pesant sur le pâturage. Même dans des écosystèmes « naturels », notamment certaines savanes africaines, l'homme régule également les populations d'animaux dans un but de conservation de l'écosystème. L'homme peut aussi avoir un rôle sur les sols et notamment sur l'érosion de par la construction de routes ou autres chemins où l'eau se concentre (Poesen *et al.* 2003, Valentin *et al.* 2005).

Différents modèles ont été décrits par House *et al.* (2003) pour expliquer les (dés)équilibres « arbre-herbe » dans les pâturages :

1) La séparation des niches : les espèces ligneuses et herbacées occupent des niches distinctes et partitionnent les ressources. Une partition spatiale est expliquée par l'hypothèse de la double couche de Walter (1971) où les espèces ligneuses ont accès à de l'eau en profondeur et les espèces herbacées utilisent l'eau des premiers horizons du sol. Une partition temporelle, variation interannuelle, est également possible si les facteurs favorisant les espèces herbacées s'expriment à des périodes différentes de celles où s'expriment les facteurs favorisant les espèces ligneuses.
2) Une compétition équilibrée : ce modèle s'oppose au précédent. Les espèces ligneuses et herbacées ne partitionnent pas les ressources mais sont en compétition. Les compétitions intra-spécifiques (arbre-arbre et herbe-herbe) seront prépondérantes sur les compétitions inter-spécifiques (arbre-herbe).
3) L'exclusion compétitive : elle éloigne le système d'un équilibre où arbres et herbes coexistent. Elle suppose qu'un des deux types d'espèces préempte et monopolise l'ensemble des ressources conduisant à l'élimination du deuxième type d'espèce. A long terme, le système évolue alors soit vers une zone boisée soit une prairie dominée par les herbacées. Les facteurs de perturbation tels que le feu où l'herbivorie jouent un rôle important sur la capacité des espèces ligneuses ou herbacées à dominer.
4) Possibilité d'existence de plus d'un état stable : l'hétérogénéité spatiale et temporelle des ressources disponibles et des facteurs de perturbation sont inclus dans des modèles d'équilibre et induisent des ratios « arbre-herbe » différents pouvant exister sur un site donné à différentes périodes. La modification des ressources ou des perturbations peut altérer les interactions « arbre-herbe » et déplacer le ratio d'un point d'équilibre à un autre et transformer une savane en forêt ou en prairie.

Sankaran *et al.* (2004) définissent deux types de modèles : des modèles fondés sur la compétition « arbre-herbe » pour l'acquisition des ressources (Walter 1971, Eagleson and Segara 1985, Van Langenveld *et al.* 2003) et des modèles fondés au contraire sur la démographie des arbres et les facteurs clés de perturbation limitant les différents stades de croissance des arbres (de la germination à la mort) (Higgins *et al.* 2000, Jeltsch *et al.* 1996, 1998, 2000).

Quels que soient la classification et le découpage de ces modèles, aucun modèle ne peut expliquer à lui seul la diversité des systèmes « arbre-herbe » et des situations d'invasion rencontrées. C'est très certainement une combinaison de ces modèles associée à d'autres facteurs clés évoluant à des échelles de temps et d'espace variables (Scholes et Archer 1997) qu'il faut intégrer pour développer une compréhension globale des causes et mécanismes de l'invasion ligneuse.

II. Les conséquences de l'invasion ligneuse dans les pâturages

Une fois implantés, les arbres vont également influencer l'environnement existant, c'est-à-dire les sols, le couvert herbacé et les herbivores (Fig. 1).

Conséquences sur les sols : les arbres ont des conséquences multiples et antagonistes sur les différentes propriétés du sol. Les arbres, particulièrement en climat aride et semi-aride, ont un effet d'ombre et modifient le microclimat sous-canopée diminuant la température et l'évapotranspiration des sols (Belsky *et al.* 1989, Vetaas 1992). Les légumineuses, comme les acacias ont souvent été mentionnées pour leur effet d'augmentation de la teneur en azote du sol (Wiegand *et al.* 2005, Treydte *et al.* 2007). Par contre l'effet des arbres sur le stockage du carbone dans le sol est variable et dépend du climat : l'invasion en régions arides favoriserait une augmentation du carbone dans le sol alors que dans les régions plus humides elle diminuerait le stockage de carbone dans le sol (Jackson *et al.* 2002). Les teneurs en nutriments sont souvent plus élevées sous la canopée des arbres (Abule *et al.* 2005). La litière provenant des feuilles d'arbres peut modifier les propriétés chimiques du sol, telle la capacité d'échange cationique par exemple (Trinogga 2010). Les flux d'eau sont fortement modifiés par la présence d'arbres. Les arbres, en fonction de leur morphologie, vont modifier l'arrivée de l'eau au sol par interception et écoulement le long du tronc (Mauchamp et Janeau 1993, Dunkerley 2002, Liang *et al.* 2009) ou du fait de la traversée de la canopée (Martinez-Meza et Whitford 1996, Carlyle-Moses 2004). La captation des pluies par la canopée et son évaporation va aussi diminuer la quantité d'eau arrivant au sol. Les arbres pompent de l'eau (Eggemeyer *et al.* 2008, Sher *et al.* 2010, Reinsch *et al.* sous presse); ils peuvent la redistribuer par un effet d'ascenseur hydraulique dans différents horizons du sol (Ludwig *et al.* 2003). Ils peuvent augmenter l'infiltration de l'eau dans le sol (Martinez-Meza et Whitford 1996) et l'humidité du sol sous-canopée (Belsky *et al.* 1989, Vetaas 1992) ou au contraire augmenter le ruissellement (Petersen et Stringham 2008). Les arbres modifient à la fois les processus hydrologiques de surface et de subsurface jusqu'à l'échelle du bassin versant (McCole et Stern 2007, Huxman *et al.* 2005). L'ensemble de ces processus vont ainsi jouer un rôle sur l'érosion hydrique des sols (Reid *et al.* 1999, Ludwig *et al.* 2005, Martinez-Casasnovas *et al.* 2009). Dans certains cas, l'invasion a été associée à une augmentation de l'érosion en nappe due à une augmentation du ruissellement (Reid *et al.* 1999, Petersen et Stringham 2008, Muñoz-Robles *et al.* 2011). La coupe d'arbustes (*Mesquite Prosopis velutina Woot.*) a été associée à une diminution des pertes en sol et à une réduction de l'avancement de têtes de ravine (Martin et Morton 1993). Ces résultats étaient principalement liés à l'amélioration du couvert herbacé après la coupe des arbustes. Cependant, Muñoz-Robles *et al.* (2010) n'ont pu montrer un effet direct clair de l'invasion ligneuse sur l'érosion en ravine.

Conséquences sur le couvert herbacé : Si certaines études ont montré des effets négatifs sur la biomasse du couvert herbacé (Hoffman et Ashwell 2001, Lett et Knapp 2003), d'autres ont montré un effet neutre (Abule *et al.* 2005, Treydte *et al.* 2007, Ludwig *et al.* 2004, 2008). Certains arbres, notamment les légumineuses, tels les acacias, ont des effets positifs sur la qualité de la strate herbacée sous-canopée (Treydte *et al.* 2007, Ravi *et al.* 2010). Les « îles de la fertilité », comme peuvent être appelés certains arbres envahissants, voient leur couvert herbacé sous-jacent s'enrichir en nutriments, protéines, énergie, digestibilité des feuilles fraiches ainsi qu'une diminution de la teneur en fibres (Ludwig *et al.* 2008). Les espèces herbacées voient souvent leurs compositions modifiées par la présence d'arbres (Tisdale *et al.* 1993, Ruthven 2001, Fynn *et al.* 2005).

Conséquences sur les herbivores : les arbres fournissent un fourrage aux brouteurs mais aussi aux paisseurs qui se nourrissent des gousses dans le cas d'acacias par exemple. Cependant, si les effets sur les sols et le couvert herbacé sont sujet à controverses, il existe une unanimité sur l'effet de l'invasion sur les herbivores : au-delà d'une densité seuil, le pâturage devient impénétrable aux animaux et la surface de pâture est réduite de façon importante (Smit 2004). L'usage d'origine du pâturage n'est alors plus possible.

Cet exposé démontre les conséquences contrastées des ligneux sur l'écosystème. Elles font intervenir de nombreux processus et elles dépendent également de l'échelle spatiale considérée (Riginos *et al.* 2009b). A petite échelle, celle de l'arbre, des effets positifs sur le couvert herbacé et les nutriments du sol sont le plus souvent mentionnés. Tandis qu'à plus grande échelle, celle du paysage, les effets peuvent s'inverser.

III. Démarches et problématiques

L'invasion ligneuse dans les pâturages est une thématique complexe faisant intervenir de nombreux paramètres et facteurs comme nous l'avons vu précédemment. L'étude d'un tel système nécessite donc une approche multi-facteurs et multi-échelles si nous voulons apporter une contribution pertinente à la compréhension des mécanismes qui régissent l'invasion ligneuse. Malgré les nombreuses études citées ci-dessus, des interrogations subsistent concernant à la fois les facteurs de contrôle de l'invasion et ses conséquences sur l'écosystème. L'une des seules études à large échelle (Sankaran *et al.* 2008) intégrant les données de plus de 850 sites en Afrique a pu mettre en évidence une séparation climatique des processus liés à l'invasion ligneuse (Sankaran *et al.* 2005). Dans les zones de précipitations moyennes annuelles (MAP) inférieures à 650 mm, les densités maximales d'arbres sont limitées par la pluie et évoluent en fonction de celle-ci. Le feu et l'herbivorie modifient cependant les densités d'arbres en dessous du seuil maximal. Dans des zones de MAP supérieures à 650 mm, l'invasion est moins limitée par l'eau, et les facteurs de perturbations sont indispensables au maintien d'un équilibre « arbre-herbe ». Les conséquences de l'invasion semblent également plus controversées dans ces zones plus humides où les processus hydrologiques sont exacerbés par les précipitations et l'éventuelle présence de ravines. Dans ce contexte, peu d'études associant l'érosion en ravine et l'invasion ligneuse ont été réalisées (Martin et Morton 2003, Muñoz-Robles *et al.* 2010) malgré l'importance et les conséquences de ces deux phénomènes et leurs possibles interactions par l'intermédiaire du substrat « sol ». C'est donc à ces zones plus humides que nous allons nous intéresser afin de comprendre et compléter les connaissances des interactions et mécanismes intervenant dans l'invasion ligneuse de pâturages ravinés. Cette étude ne vise pas à répondre à la grande interrogation de l'équilibre « arbre-herbe », mais à proposer des résultats et conclusions qui permettront de faire avancer les connaissances et d'apporter une meilleure compréhension de ce système.

Les principales questions abordées dans ce mémoire sont donc orientées à la fois sur les facteurs de contrôle de l'invasion ligneuse et ses conséquences sur des pâturages ravinés à différentes échelles d'espace et de temps. En prenant l'exemple d'un pâturage d'Afrique du Sud raviné envahi par une espèce d'*Acacia* endémique, les questions suivantes seront abordées :

1) Comment l'invasion ligneuse et l'érosion en ravine ont-elles évolué à l'échelle du bassin versant au cours des 64 dernières années? Notamment, comment l'hydrodynamique et les propriétés du sol interviennent-elles sur la répartition spatiale des acacias?
2) Comment les principaux facteurs de contrôle de l'invasion agissent-ils sur les premiers stades de la population d'*Acacia*?
3) Quel est le lien entre la population d'*Acacia* et les ressources en eau du sol, et particulièrement les profondeurs de prélèvement d'eau?
4) Quelles sont les conséquences de l'invasion ligneuse sur l'érosion en ravine et sur les propriétés du couvert herbacé et du sol?

C'est à partir d'une démarche pluridisciplinaire que ces questions seront traitées.

Après cette introduction, le site et le contexte d'étude seront présentés ainsi qu'un aperçu des méthodes utilisées dans les différentes expériences de cette étude. Des résultats obtenus à l'échelle du bassin versant permettront de répondre à la première question. Les facteurs de contrôle de l'invasion ligneuse seront ensuite mis en exergue en répondant aux questions 2 et 3 avant de traiter les conséquences de l'invasion ligneuse dans un pâturage raviné. Une synthèse des résultats permettra d'exposer les principales conclusions de ce travail et de discuter des perspectives à envisager dans le cadre d'une meilleure compréhension de l'invasion ligneuse dans les écosystèmes pâturés.

Chapitre 1. Un exemple de pâturage raviné et envahi en Afrique du Sud

Pâturage de la communauté de Potshini, KwaZulu-Natal (Afrique du Sud), en fin de saison sèche (septembre 2007).

I. Choix du site d'étude : situation géographique et climat

Afin de répondre aux objectifs de cette étude, l'ensemble du travail de terrain a été réalisé sur une prairie naturelle sud-africaine fortement ravinée présentant une invasion ligneuse mono spécifique par l'*Acacia sieberiana* var. woodii (Burtt Davy) Keay & Brenan. Ce pâturage communautaire rattaché au village de Potshini se situe à 8 km au sud-est de Bergville (28° 48' 37" S; 29° 21' 19" E), ville rurale de la province du KwaZulu-Natal en Afrique du Sud (Fig. 2). Le bassin versant choisi orienté nord (donc au soleil car nous sommes dans l'hémisphère sud) représente la partie la plus importante du pâturage communautaire et il est situé à une altitude de 1217 m à 1452 m et représente une surface de 2.5 km^2.

Ce site a été choisi pour plusieurs raisons :

1. Ce bassin versant est situé au sein du bassin versant de la Tugela couvrant une surface de près de 30 000 km^2 (Schulze *et al.* 2004) ayant un impact hydrologique majeur sur la région du KwaZulu-Natal.
2. Potshini est un village représentatif de l'ensemble du piémont du Drakensberg, où sont implantés de nombreux villages traditionnels vivant en communauté.
3. Ce pâturage communautaire est soumis à une forte pression anthropique et l'invasion pose un problème clairement identifié par les éleveurs.
4. L'université du KwaZulu-Natal et particulièrement le laboratoire d'hydrologie, *Bioresources Engineering and Environmental Hydrology* (BEEH), au sein duquel l'équipe IRD-Bioemco est affectée, a été introduit au sein de la communauté de Potshini en 2000 et entretient depuis de bonnes relations permettant de réaliser des expérimentations *in situ* en accord et avec la participation de la communauté.
5. L'accès relativement aisé et peu éloigné du site a facilité l'étude de l'invasion ligneuse associée à l'érosion en ravine.

La zone d'étude est localisée dans un climat semi-humide semi-tropical d'hémisphère sud avec quatre saisons guidées principalement par un été chaud et pluvieux (octobre-avril) et un hiver froid et sec (mi-septembre). Le printemps et l'automne sont beaucoup moins marqués. La pluviométrie annuelle calculée sur les 65 dernières années est de 745 mm (Fig. 3) et la température moyenne annuelle de 13 °C (Schulze 1997). L'évaporation potentielle est entre 1600 et 2000 mm par an (Guy et Smith 1995). Les gelées sont fréquentes en hiver et la grêle occasionnelle en été.

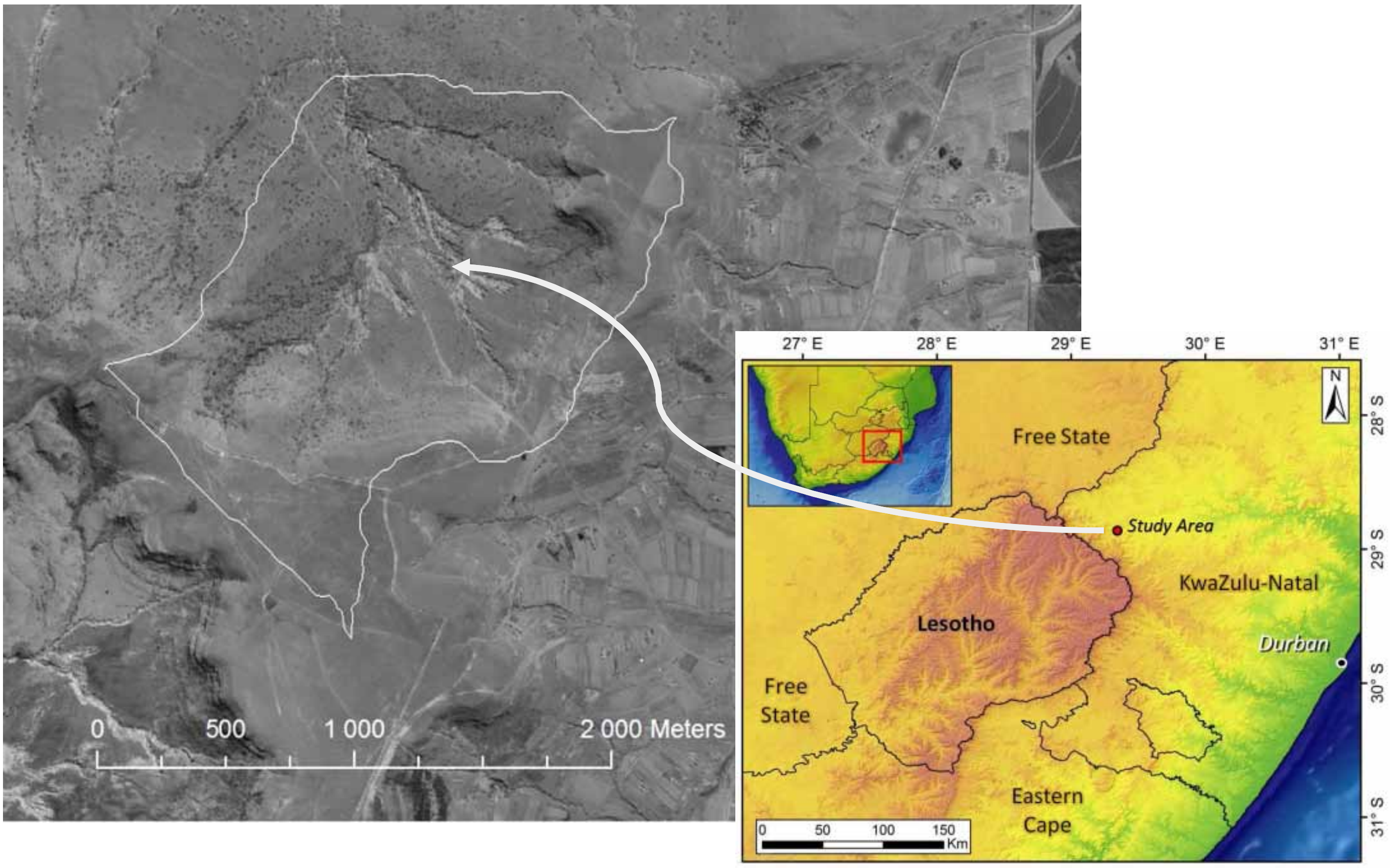


Figure 2. Localisation du site d’étude dans la communauté de Potshini en Afrique du Sud.

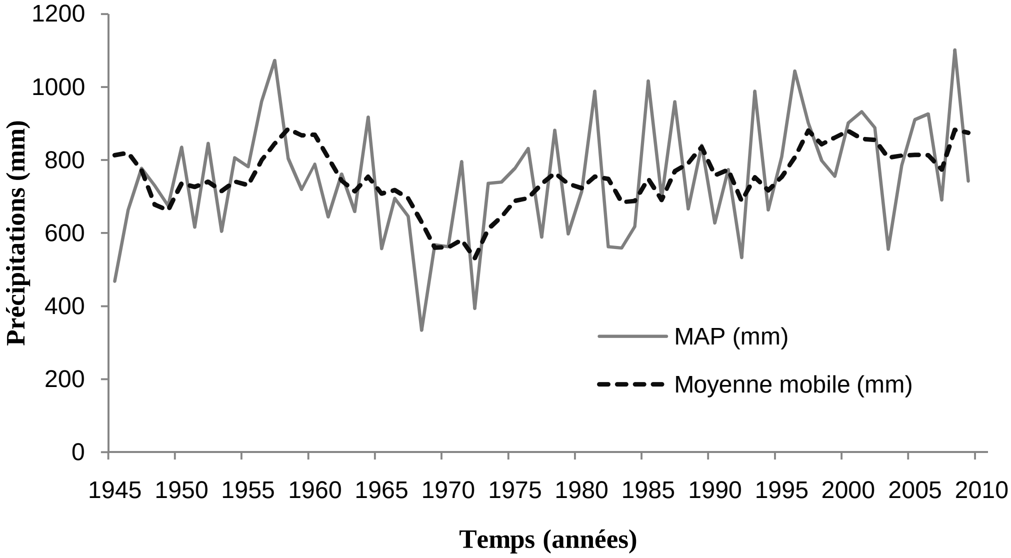


Figure 3. Précipitations moyennes annuelles (MAP) (mm) et moyenne mobile sur 5 ans (mm) entre 1945 et 2009 pour le site d’étude.

II. Les sols et la géologie du site

Les sols de Potshini se sont formés à partir d'une formation géologique des groupes Beaufort et Ecca appartenant au groupe Karoo datant de la période du Permo-Triasique. La roche mère s'est déposée sous forme de successions horizontales avec une alternance de couches dures et résistantes (grès) et de couches moins dures et plus sensibles à l'érosion, à grains plus fins tels les schistes, argilites et siltites (King 2002). Des dépôts de colluvions non-consolidés du Pléistocène complètent cette géologie et ont comblé principalement les fonds de vallée. Ces colluvions sont particulièrement susceptibles à l'érosion en ravine qui indente le paysage depuis des millénaires (Botha 1994). De nombreux filons intrusifs de dolérite du Karoo affleurent à plusieurs endroits visibles par la présence de blocs rocheux rougeâtres de petites tailles (10 cm à 50 cm de diamètre) et conduisant à des sols de couleur rouge.

Les sols formés sur cette géologie sédimentaire rythmée sont de type Acrisols dans les hauts de versant et de type Luvisol dans les milieux et bas de versant (W.R.B 1998). Il s'agit de sols duplex avec une très nette distinction d'un horizon A (environ 0-40 cm) et B (environ 40-90 cm) (Fig. 4). L'horizon A est cohésif, de couleur gris-marron (10YR 4/1 to 10YR 4/3) avec de nombreuses racines fines et moyennes et une activité biologique importante. L'horizon B sous-jacent est de type Bt et/ou Bw accumulant jusqu'à 50 % d'argile, principalement des illites. Cet horizon est plus cohésif et dur. Les analyses détaillées de trois profils de sol le long d'une toposéquence sont présentées en annexe 1.

La superposition d'une roche mère dispersive que sont les colluvions de bas de versant (horizon C), et d'un sol duplex présentant une différence de perméabilité entre l'horizon A et B où les processus de gonflement-retrait des argiles induisent des fissures propices à la concentration d'eau, favorise la formation de phénomène d'érosion interne au sol (suffosion) avec la formation de drains ou tunnels de subsurface (Imeson et Kwaad 1980, Beckedahl 1998, Verachtert *et al.*, 2010). La figure 5a est un exemple d'effondrement du toit de l'un de ces tunnels (« pipes » en anglais) observables dans le bassin versant. La figure 5b montre un tunnel également, mais il s'agit de l'extrémité de sortie du tunnel débouchant en bas de versant dans la ravine. Les ravines présentes sur le site forment un réseau d'écoulement d'eau temporaire et peuvent dépasser 10 m de profondeur, 50 m de largeur et plusieurs centaines de mètres de longueur.

Figure 4. A gauche, bord de ravine présentant une limite nette entre l'horizon A et B. A droite, profil de sol rafraichi et humidifié pour des mesures géo-électriques au milieu de la toposéquence où sont également visibles l'horizon A plus sableux et l'horizon B plus argileux.

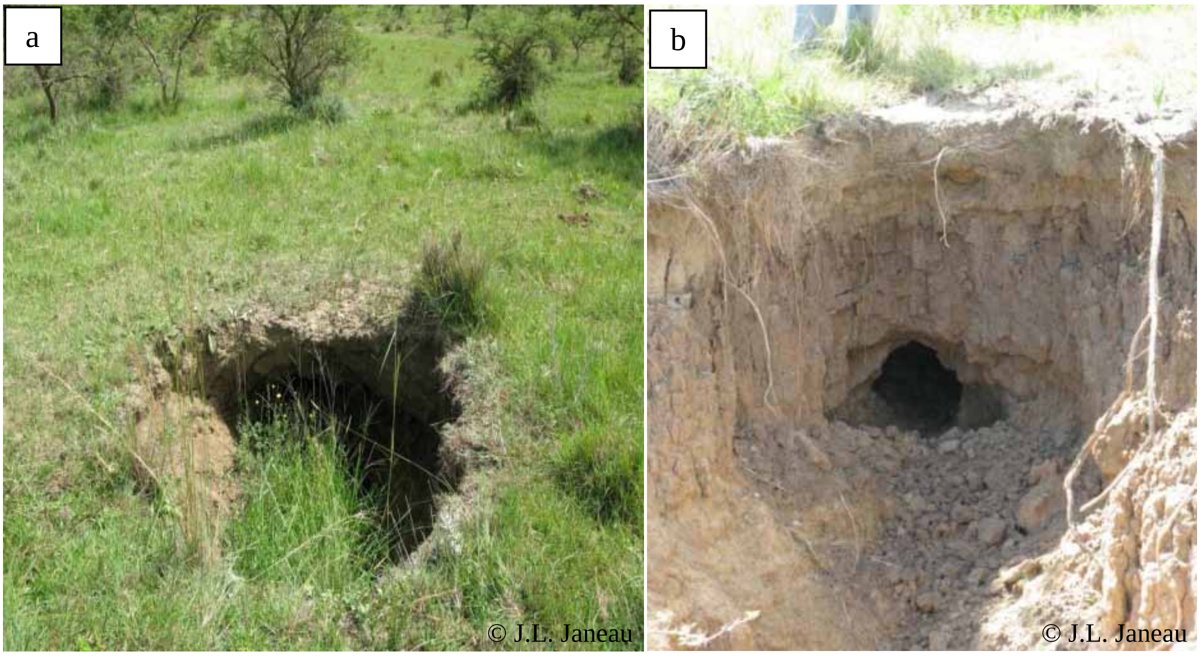


Figure 5. a) l'effondrement du toit d'un tunnel (2 m de large) en amont de la ravine. b) l'extrémité d'un tunnel situé en surface de l'horizon C et débouchant dans la ravine.

III. Composition de la végétation : strates herbacée et arborée

La zone de Potshini est située dans le biome « *Northern KwaZulu-Natal moist grassland* » (Mucina et Rutherford 2006), le biome des prairies naturelles humides du nord du KwaZulu-Natal. Ce biome est adjacent au biome de savane, très proche géographiquement (Fig. 6). Le biome des prairies humides est dominé par deux espèces herbacées pérennes principales que sont *Themeda triandra* Forssk et *Hyparrhenia hirta* (L.) Stapf. Toutefois, *Themeda triandra* est très appréciée du bétail (Oudtshoorn 2004) et peut facilement voir sa présence diminuer si la charge de bétail est trop importante. C'est le cas à Potshini puisque les principales espèces herbacées (Poacées) présentes en 2009 étaient par ordre d'importance : *Hyparrhenia hirta*, *Sporobolus africanus* (Poir.) Robyns & Tournay, *Digitaria longiflora* (Retz.), *Paspalum scrobitulatum* (L.), *Eragrotis plana* Nees, *Eragrotis curvula* (Schrad.) Nees, *Themeda triandra*, and *Cymbopogon excavatus* (Hochst.) Stapf ex Burtt Davy.

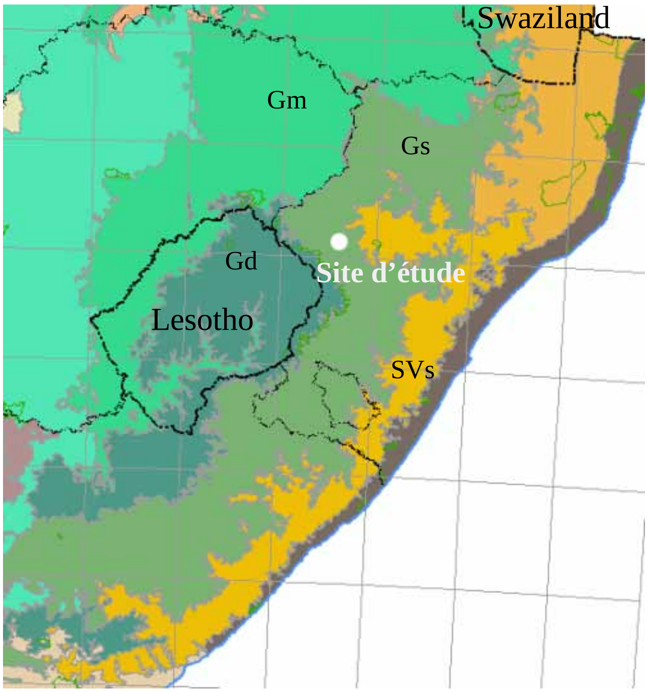


Figure 6. Carte des biomes de l'est de l'Afrique du Sud, adaptée de Mucina et Rutherford (2006).

En dehors des Poacées, plus de 120 espèces herbacées ont été identifiées sur le site. La plus représentée n'est pas endémique, *Richardia brasiliensis* (Moq.) (Gomez Rubiaceae), tout comme *Centella asiatica* (L.) (Apiaceae). D'autres sont endémiques telles que *Sida dregei* Burtt Davey (Malvaceae), *Vernonia natalensis* (Sch.Bip. ex Walp) (Asteraceae), *Senecio inaequidens* DC. (Asteraceae), *Hibiscus pedunculatus* L.f. (Malvaceae).

L'espèce ligneuse à épines *Acacia sieberiana* var. woodii (Burtt Davy) Keay & Brenan (Fabaceae, Mimosoideae) (Fig. 7) qui est à l'origine de l'objet d'étude principal de ce travail envahit ce pâturage, ainsi qu'une surface importante des pâturages du KwaZulu-Natal.

C’est une espèce endémique (Pooley 1993) d’où la dissociation en anglais du terme « *encroachment* » et « *invasion* ».

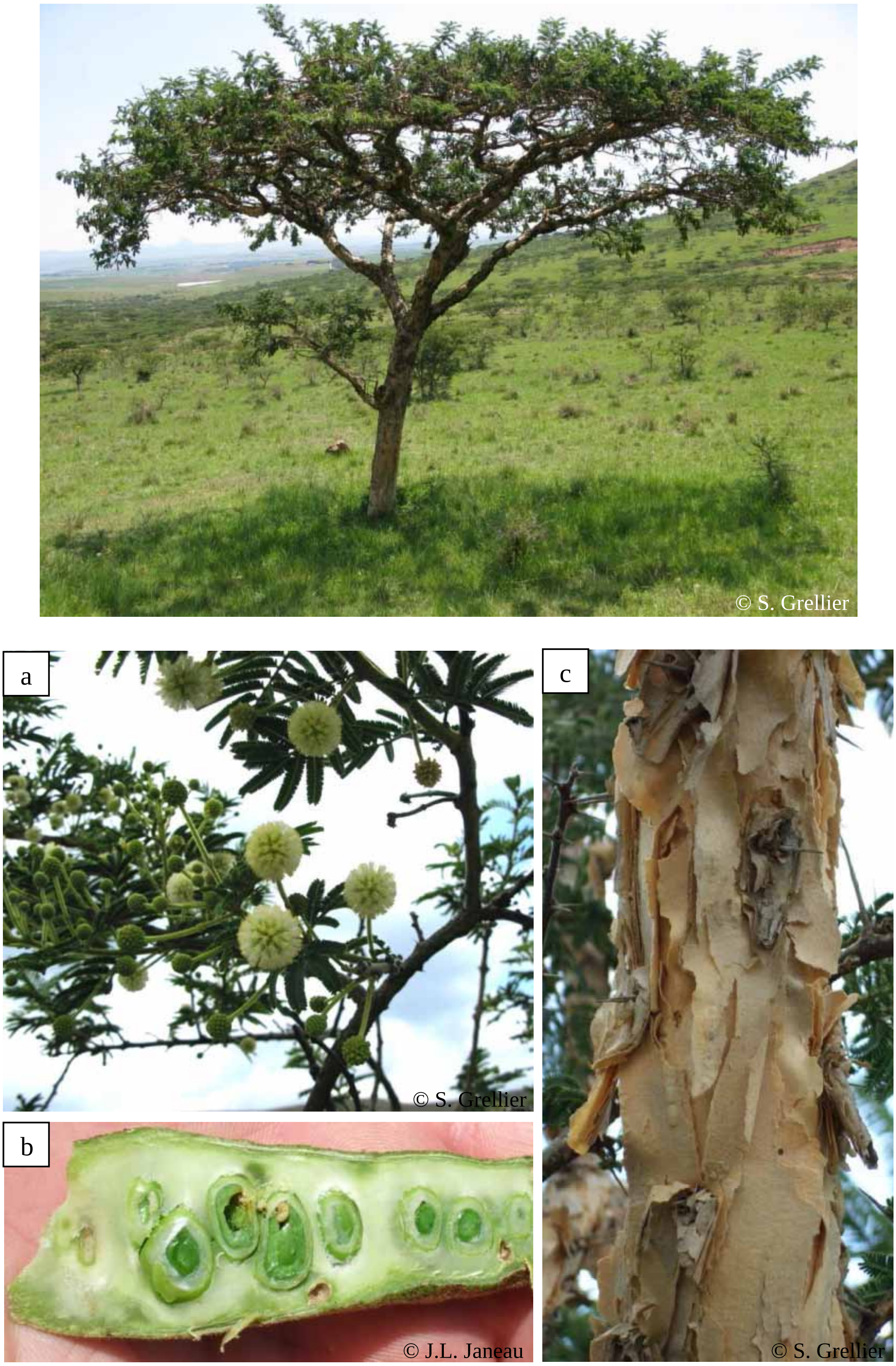
Les acacias sont représentés par environ 1300 espèces dans le monde dont 960 seraient natives d’Australie malgré la première description en Afrique par Carl Linnaeus en 1773. Environ 44 espèces d’acacias sont recensées en Afrique du Sud. Les acacias d’Afrique présentent généralement des épines alors qu’en Australie, il s’agit d’acacias non épineux. On trouve quelques espèces d’acacias en Europe, dans le sud de l’Asie et en Amérique principalement dans les régions tropicales à tempérée-chaudes. Les acacias sont des légumineuses qui, en symbiose avec des bactéries (rhizobium) localisées au niveau de nodules racinaires, sont capables de transformer l’azote atmosphérique (N_2) en ammoniac (NH_3) directement assimilable par les plantes et éventuellement d’enrichir le sol en NH_3.

Acacia provient du grec « akantha » signifiant épine. Le nom *sieberiana* a été donné d’après le nom de Franz Sieber (1789-1844), un botaniste voyageur et collectionneur de plantes. *Acacia sieberiana* est aussi appelé « *paperbark acacia* » ou acacia à écorce de papier de par le délitement de son écorce en « feuille de papier » (Fig. 7). Il est présent en Afrique du Sud, mais aussi au Swaziland, au Zimbabwe, au nord et à l’est du Botswana, au nord de la Namibie et dans l’Afrique tropicale au nord de l’Ethiopie. Il présente un système racinaire dimorphe avec de nombreuses racines latérales situées dans les premiers horizons du sol et un pivot racinaire profond. *A. sieberiana* est une espèce caduque qui perd ses feuilles en milieu de saison sèche (juin) et qui fleurit en septembre (Fig. 7). *A. sieberiana* forme des gousses déhiscentes au cours de la saison humide.

L’odeur assez forte des gousses attire certains animaux. Les scarabées *bruches* (Coleoptera : Bruchidae) sont des prédateurs de graines d’*Acacia* dont les larves se nourrissent (Coe et Coe 1987; Or et Ward 2007) (Fig. 7). Ces derniers, ainsi que des abeilles, papillons ou thrips (bête d’orage) attirent des oiseaux insectivores comme l’*Apalis à gorge nue* (*Bar-throated Apalis),* ou le *Souimanga noir, à collier,* ou *à ventre blanc (White-bellied, Black* et *Collared Sunbird).* Les bovins, caprins, ovins raffolent de ces gousses riches en protéines et en sont des disséminateurs privilégiés (Coe et Coe 1987) tout comme certains petits mammifères tels les rats (Goheen *et al.* 2004, Goheen *et al.* 2010).

L’utilisation de *A. sieberiana* dans certaines cultures africaines (en centre Afrique notamment) repose sur des décoctions d’écorces et/ou racines contre l’inflammation des voies urinaires. Les feuilles, l’écorce et la résine sont utilisées comme remèdes contre les rhumes, diarrhées, hémorragies et infections oculaires.

Les informations fournies ci-dessus sur *A. sieberiana* proviennent en partie d’informations disponibles sur http://www.plantzafrica.com/plantab/acaiasieber.htm de Joffe (2003).



© S. Grellier
© S. Grellier
© J.L. Janeau
© S. Grellier

Figure 7. Vue de différents organes de l'*Acacia sieberiana* var. woodii. (a) les inflorescences en forme de globes fleurissant en septembre; (b) une coupe transversale dans la longueur de gousse d'*A. sieberiana* renfermant la larve d'un scarabée « *Bruchid* » ; (c) l'écorce de l'*A. sieberiana* se délitant en feuille de papier.

IV. Contexte agro-socio-économique de la communauté de Potshini

Les habitants de Potshini vivent selon un mode de vie traditionnel zoulou. L'habitat est regroupé par famille (environ 240 à Potshini) et chaque famille possède une ou plusieurs parcelles de terre. Sur chaque propriété, sont associés le lieu de vie et des parcelles agricoles. Chaque famille cultive sur des petites surfaces (0.5 à 2 ha) du maïs (*Zea mays*) et des haricots (*Phaseolus vulgaris*) et parfois d'autres légumes notamment en lien avec les recherches menées par l'Université du KwaZulu-Natal sur les systèmes d'irrigation à petite échelle (Kongo et Jewitt 2006). L'élevage est également associé à ces parcelles sur lesquelles sont élevés des volailles et parfois des porcs. Ces zones de cultures et d'habitats sont regroupées dans la partie aval du bassin versant où les pentes sont plus faibles et les terres plus fertiles. La zone haute du bassin versant est réservée exclusivement au pâturage des bétails (bovins et caprins) à l'aide d'une clôture séparant les deux zones. Il s'agit donc d'un pâturage communal pour l'ensemble des différents éleveurs de la communauté. Un comité de gestion des pâturages regroupe quelques éleveurs (les plus influents et expérimentés). L'organisation est relativement simple et se fait selon une rotation en deux périodes : pendant la période de culture du maïs et haricots sur les parcelles agricoles, le bétail est maintenu sur les pâturages pendant 8 mois environ, de novembre à juin, qui correspondent à l'été et l'automne sud-africain. Aussitôt que le maïs est récolté en juin, le bétail est retiré du pâturage et il pâture sur les résidus de culture jusqu'à ce que l'herbe du pâturage soit de nouveau accessible après les premières pluies d'octobre. Cette deuxième période dure environ 4 mois de juillet à octobre. La gestion du feu est quasi inexistante (du moins pour les 5 dernières années) laissant le pâturage face aux aléas des feux naturels et provoqués de façon anarchique.

La zone d'étude envahie par *A. sieberiana* est située dans un bassin versant adjacent à celui des zones habitables et de cultures. Il a été mis officiellement à disposition de la communauté par le gouvernement en 2002. Cependant, il semble que la communauté avait accès bien avant cette date à ce pâturage qui communique directement avec la zone initiale de pâturage. L'ensemble du pâturage de la communauté est donc réparti sur deux bassins versants dont la surface la plus importante est située sur la zone d'étude et pour lequel il n'y a donc pas d'habitat en aval puisqu'il est réservé exclusivement au pâturage. Malgré cette augmentation significative de surface à vocation pastorale, la quantité de tête du bétail semble toujours trop importante (estimée à plus de 1 000 têtes en 2010) pour la surface disponible (d'un total d'environ 700 ha).

L'agriculture n'est cependant pas la première source de revenus pour la communauté, même si la possession de vaches est ancrée dans une forte tradition. Les vaches servent de dot pour les mariages. Entre 8 et 12 vaches peuvent être données à la famille de la mariée. La vente d'une vache sert également à aider un proche en cas de difficultés (enterrements, maladies, scolarité, etc.). Même si la possession de vaches à son importance culturelle, 85 %

des familles perçoivent des aides sociales du gouvernement et 45 % bénéficient de salaires provenant de membres de la famille partis travailler en ville à Durban où à Johannesburg principalement (Mudhara *et al.* soumis). En effet, l'Afrique du Sud n'échappe pas à l'exode rural et de nombreux jeunes partent pour les villes dans l'espoir de trouver un travail. Cet exode des jeunes travailleurs, associé à un taux de SIDA qui atteint des records dans le KwaZulu-Natal (entre 10 et 20 % de la population globale en 2010) laisse les villages peuplés de femmes seules et de jeunes enfants qui ont alors la charge des troupeaux.

Juxtaposé à ce village traditionnel, la propriété agricole d'un « commercial farmer », exploitant agricole d'origine européenne, occupe une large partie de la zone aval du bassin versant. Il utilise les techniques de pointe de l'agriculture moderne. C'est donc dans ce paysage culturel multiple qu'il faut appréhender l'étude de l'invasion d'arbres dans les pâturages ravinés qui touchent à la fois les pâturages communaux traditionnels, les pâturages extensifs des grands exploitants et les savanes de zones de réserves naturelles.

Chapitre 2. Aperçu des méthodes utilisées

© J.L. Janeau

Survol et prise de photographies aériennes grâce au drone Pixy-IRD.

Les méthodes utilisées lors de ce travail sont décrites dans les chapitres suivants de ce mémoire qui est constitué d'une série d'articles dont trois soumis à des revues scientifiques. Cependant, la multidisciplinarité de ce travail a fait intervenir un nombre important d'outils pour lesquels des précisions sont apportées dans le présent chapitre. Cette partie explicite également le choix de certaines méthodes et illustre les expériences mises en place *in situ*, la collecte de données de terrain et leur traitement. Ce chapitre fait également mention de l'obtention de données écologiques encore non incluses dans des articles mais qui feront l'objet de traitements ultérieurs.

I. Spatialisation et cartographie

1. L'obtention et le traitement de photos aériennes

Afin de pouvoir étudier le système dans son ensemble et de couvrir la plus longue période possible, il était nécessaire de disposer d'une couverture photographique aérienne de la zone la plus récente. Le gouvernement Sud-Africain possède un département à Cape Town, le « National Geospatial Information (NGI), Department of Land Affairs » qui est en charge de survoler le pays et de fournir des photographies aériennes. Nous disposions d'une photographie de 2006 de Potshini, mais il semblait intéressant d'avoir une photographie plus récente prise à basse altitude qui permette d'observer plus de détails, notamment la population d'arbres et les « petits » arbres inférieurs à 1 m^2 de surface de canopée qui ne sont pas visibles sur des photos à une échelle de 1/20000. C'est donc grâce à une collaboration inter-équipes IRD que Jean-Louis Rajot et Jean Asseline sont venus à Potshini avec un paramoteur radio télécommandé appelé le « Pixy » qui répondait à nos attentes. (Fig. 8). A l'aide d'une caméra, d'un appareil photo et d'un GPS embarqués, il est alors possible de visualiser ce que le Pixy survole, de prendre des photos grâce à un déclencheur et d'enregistrer la trajectoire précise du Pixy ainsi que son altitude. Nous avons donc pu obtenir plusieurs jeux de photos prises à différentes altitudes (environs 2000 photos) et avec différentes focales (18 à 55 mm). Les photos prises aux altitudes les plus élevées (autour de 400 m) ont permis d'avoir une vue globale du bassin versant qui pouvait être comparée aux photos antérieures prises par avion par le NGI en 1945, 1962, 1976, 1985, 2001 et 2006. Les photos aux plus faibles altitudes, entre 30 et 100 m offraient une vue de certaines zones du bassin versant avec tous les détails escomptés : distinction d'un rocher et d'une termitière de 20 cm de diamètre, observation des petits acacias (Fig. 9).

Le travail consiste ensuite à géoréférencer et rectifier les photos pour obtenir une seule scène de la zone. La position de la caméra sur le Pixy n'étant pas toujours horizontale (à cause des vents et des ascendances), de fortes déformations sur les photos peuvent apparaitre. Ceci nécessite un redressement des photos, réalisé grâce à une coopération avec Jaco Kemp, sud-africain en post-doctorat à l'université de Stellenbosch. La prise de points GPS au sol de grande précision et identifiables sur chaque photo est alors nécessaire pour redresser les photos une à une à raison d'un minimum de 4 points par photo (aux extrémités de la photo si possible où les déformations sont les plus importantes). Ceci est possible grâce à un GPS de grande précision (LEICA GRX1200), le DGPS « *Differential Global Positionning System* », et à la localisation *in situ* d'éléments grossiers les plus volumineux, de troncs d'arbres morts, de termitières visibles sur les photos. Ce post-traitement de rectification, géoréférencement et d'assemblage des photographies a été effectué grâce au logiciel ArcGis (ESRI 2008).

Figure 8. Décollage du Pixy sur le bassin versant de Potshini.

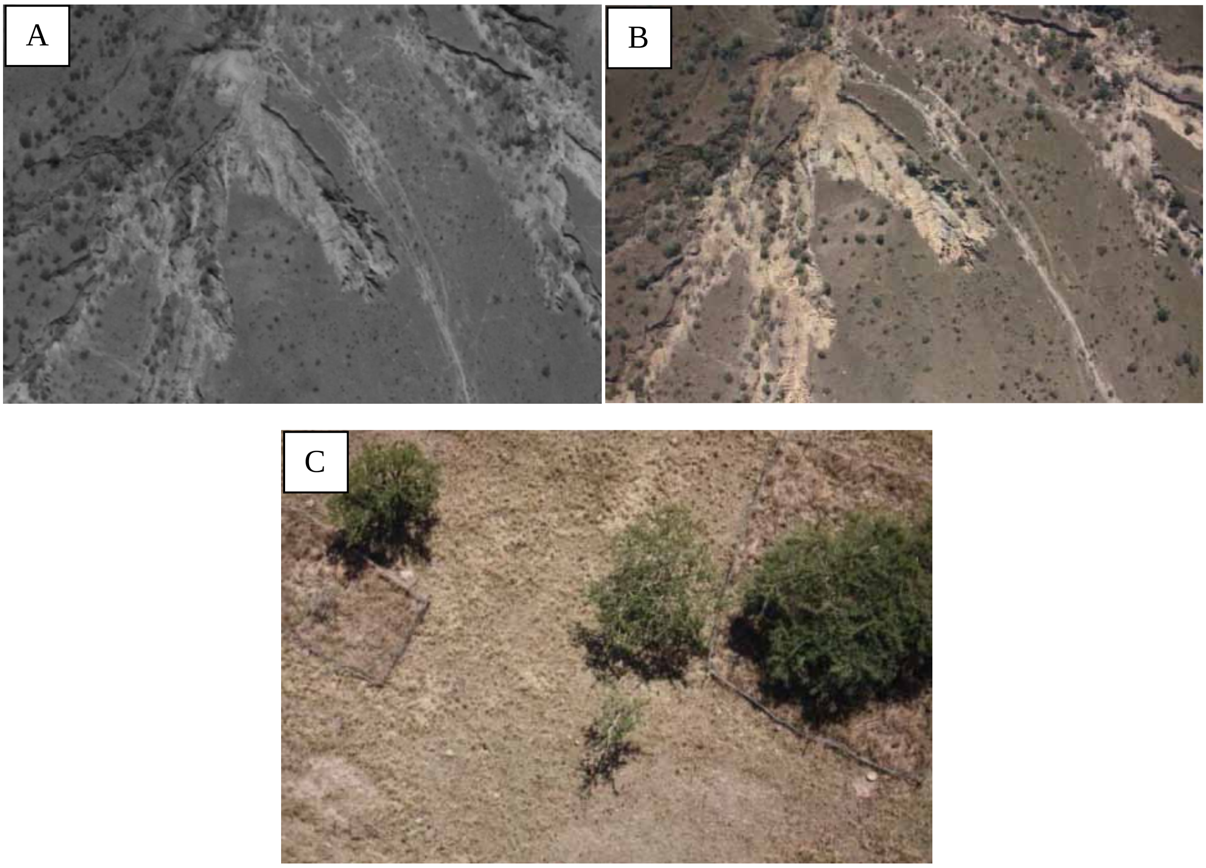


Figure 9. Vues aériennes du bassin versant prises A) par avion par NGI en 2006, B) par Pixy à 400 m du sol en 2009, C) par Pixy à 40 m du sol en 2009. La photographie obtenue par NGI a été zoomée au maximum contrairement à celles obtenue par le Pixy présentées ici brutes (non zoomées, non-rectifiées).

2. Cartographie et DGPS « *Differential Global Positionning System* »

Un des aspects importants du travail réalisé pendant ces quatre années en Afrique du Sud porte sur la spatialisation de la population d'*A. sieberiana* et des ravines. Pour appréhender cette dimension spatiale, outre les photos aériennes qui nous donnent beaucoup d'informations, la cartographie sur le terrain est aussi intéressante et d'ailleurs nécessaire comme on l'a vu dans la partie précédente pour la rectification des photos. C'est grâce à l'utilisation d'un DGPS (Leica GRX1200) que tout le travail de cartographie a été réalisé. Le DGPS consiste à utiliser simultanément deux récepteurs GPS :

- un récepteur fixe dont la position est précisément connue, ce qui permet de déterminer les erreurs des positions envoyées par les satellites (traversée des différentes couches atmosphériques, position des satellites sur l'horizon, trajets multiples des ondes notamment réflexion sur les bâtiments et les plans d'eau) ;
- un récepteur mobile que l'utilisateur déplace sur les points cartographiés (Fig. 10 et 11).

L'envoi par radio des corrections déterminées par le récepteur fixe au récepteur mobile permet une correction instantanée des points pris par l'utilisateur et une précision en X, Y et Z de moins de 1 cm en conditions optimales. Dans des conditions de terrain qui ne sont jamais optimales, la précision est plutôt de 5 cm en moyenne, à comparer avec la précision d'environ 3 m d'un GPS classique.

Le DGPS a permis l'obtention d'un modèle numérique de terrain (MNT) précis, utilisé dans le calcul de paramètres topographiques notamment liés aux ravines (*cf.* chapitre 5). Cette précision a été aussi particulièrement utile pour cartographier tous les ans les jeunes plantules d'*A. sieberiana* de moins de 20 cm de hauteur (non visibles sur les photos aériennes) qui pouvaient être localisées à seulement quelques centimètres les unes des autres et qu'il était impossible de marquer de façon pérenne sans perturber l'environnement. L'intérêt de cartographier la population d'*A. sieberiana*, outre l'étude de leur répartition spatiale présentée au chapitre 3, était de suivre la population d'*A. sieberiana* sur les trois années d'étude, de mesurer des paramètres de croissance de chaque individu sur une surface déterminée (hauteur, circonférence du tronc, nombre de gousses produites, etc.). Plus de 600 arbres de toutes tailles ont été suivis afin d'intégrer les résultats dans un modèle matriciel et pouvoir tester différents paramètres de contrôle de la population et ainsi prédire son évolution. Les résultats de ces travaux, obtenus en collaboration avec Sébastien Barot ne sont pas présentés dans ce document mais feront l'objet d'un traitement ultérieur et d'une publication. Une collaboration avec le professeur Kerstin Wiegand de l'université de Göttingen en Allemagne est en cours pour une première approche de cet aspect par l'étude de la distribution des arbres en fonction de leur stade physiologique (adulte, jeune arbre, plantule) pour comprendre les mécanismes de compétition intra-espèces à l'échelle du bassin versant.

© S. Grellier

Figure 10. Récepteur fixe (base) du DGPS LEICA toujours localisé sur le même point de référence.

© S. Grellier

© S. Grellier

Figure 11. Récepteur mobile du DGPS avec transport sac à dos à gauche pour des relevés continus et transport manuel à droite pour la prise de points précis.

II. L'éco-géophysique et ses outils

La géophysique voit son champ d'investigation s'élargir à l'éco-géophysique, une association assez récente et prometteuse de la géophysique et de l'écologie (Robinson *et al.* 2008). En vue de s'assurer de la qualité des données, ce volet a été réalisé en collaboration avec Nicolas Florsch, professeur de géophysique de l'UPMC, détaché à l'IRD à l'Université de Cape Town au moment des travaux.

La géophysique dispose de nombreux outils d'étude du sol adaptés au besoin de cette étude, notamment pour identifier les zones argileuses ou les zones de circulation d'eau qui pouvaient influencer la répartition spatiale des acacias (*cf.* chapitre 3). Les différents outils et méthodes n'étant pas tous disponibles à l'UKZN, nous avons également collaboré avec Christian Camerlynck (UPMC), Myriam Schmutz (université de Bordeaux), et Muriel Llubes (laboratoire LEGOS à Toulouse) pour avoir accès à leur expérience et à leurs outils.

Plusieurs campagnes de mesures ont été organisées durant ces trois années. Il a fallu d'abord évaluer le terrain, voir ce qu'il était possible de mesurer et d'extraire comme résultats utiles dans le cadre de l'invasion d'arbres. Pour cette raison nous avons utilisé les méthodes électromagnétiques (EM31, EM38) (Fig. 12 et 13), « *time-domain electro-magnetic* » (TDEM), « *vertical electrical soundings* » (VES) (détaillées au chapitre 3) où l'*electrical-resistivity-tomography* (ERT) dont les résultats ne sont pas présentés dans ce mémoire car ils n'apportaient pas d'avantage d'information. Trois campagnes de terrain avec l'EM38 à différentes saisons ont permis :

- d'observer les différents phénomènes relatifs au sol duplex en place ;
- de mettre au point de façon certaine le protocole qui a ensuite été réalisé avec la toute nouvelle version de l'EM38-MK2 de Geonics en provenance de Toulouse dont les nouvelles fonctionnalités facilitaient grandement l'acquisition et le traitement des données.

Les problèmes de dérives des appareils, notamment l'EM38, ont aussi été au cœur de chaque campagne et il a fallu de nombreuses améliorations pour arriver à déterminer le protocole adapté à l'obtention de résultats exploitables. C'est donc durant deux campagnes supplémentaires de février 2010 et juin 2010 que l'acquisition des données EM38 a pu être réalisée en suivant un protocole précis. La géophysique a donc eu une place importante en termes de manipulation sur le terrain qui nécessite d'être au moins trois personnes sur place à cause des protocoles et de la « lourdeur » (au sens propre et figuré) de certains appareils. Un travail important de traitement des données géophysiques a été réalisé, principalement par Nicolas Florsch.


© S. Revil-Baudard

Figure 12. EM31 (3.66 m de long) porté en bandoulière sur la hanche.


© J.L. Janeau

Figure 13. EM38-MK2 en position verticale éloigné du sol pour la calibration (maintenu sur un tube plastique non conducteur). L'appareil est porté par un manipulateur non « conducteur » et un deuxième utilisateur éloigné enregistre les données sur une mémoire de masse reliée par radio à l'EM38-MK2.

III. Méthodes empruntées de l’écologie

1. Préparation et mise en place des protocoles expérimentaux

Plusieurs expériences réalisées au cours de ce travail relèvent de l’écologie :

- l’étude des différents facteurs influençant la germination et les jeunes plantules d’acacia (chapitre 4) ;
- l’étude de l’impact des arbres sur le couvert herbacé et les propriétés du sol (chapitre 5) ;
- le suivi de la population d’*A. sieberiana* sur trois années qui a été abordé dans la première partie de ce chapitre mais qui sera traité ultérieurement.

Ces travaux ont bénéficié de l’appui de Sébastien Barot à Paris, Pascal Podwojewski et David Ward à Pietermaritzburg en Afrique du Sud.

Le choix des méthodes statistiques, des modes de prélèvement, des sites, des individus à échantillonner aléatoirement, le nombre minimal d’échantillons suffisant pour obtenir des résultats significatifs a dû être réfléchi longuement et mis en balance avec le temps imparti, les moyens financiers et humains disponibles et le contexte du terrain.

L’expérience de germination qui nécessitait de suivre 8000 graines d’acacia au cours d’une année et demi révèle certaines difficultés du terrain que nous avons pu contourner. La dégradation des clôtures par le bétail et un vandalisme fréquent de cet objet de « valeur » dans ce milieu rural nous à incité à implanter l’expérience dans d’autres conditions. Cette expérience a été menée dans un terrain adjacent au bassin versant appartenant à l’exploitant agricole « *commercial farmer* » où le bétail ne pouvait entrer et dans lequel l’accès était réduit limitant la possibilité de vol (Fig. 14 et 15).

L’expérience sur l’impact des arbres sur le couvert herbacé et les propriétés du sol (chapitre 5) a donné lieu à deux collaborations qui aboutiront à deux articles. La première avec Shaun Berry, un chercheur du *South African Sugarcane Research Institute* (SASRI) à Durban. Shaun est un nématologiste avec qui nous avons travaillé sur l’impact des acacias sur les populations de nématodes. Une deuxième collaboration avec le département des sols de l’UKZN et Pascal Podwojewski a permis de travailler sur l’impact des arbres sur la stabilité structurale des sols. Un étudiant en master sud-africain travaille sur le sujet.

Il est à noter que, conjointement à ce travail de thèse, deux autres expérimentations ont été menées et sont résumées en annexes 2 et 3 :

- ✓ l’influence des scarabées (bousiers) sur la porosité du sol ;
- ✓ l’influence du couvert herbacé sur le ruissellement et la détachabilité des sols.

Figure 14. Aperçu des 24 parcelles non brûlées de 2 m^2 juste après le semis des graines en octobre 2009.

Figure 15. Aperçu des 24 parcelles brûlées de 2 m^2 juste après le semis des graines en octobre 2009.

2. Analyses des échantillons d’herbe et de sol

La détermination des espèces herbacées et non-herbacées sur les 99 parcelles échantillonnées a bénéficié des conseils de Kevin Kirkman, professeur de Botanique de l’UKZN et du personnel de l’herbier de l’UKZN.

Une grande partie des analyses a pu être réalisée par l’UKZN mais nous avons également réalisé les mesures de digestion in vitro des feuilles de Poacées (Fig. 16) par une méthode mise au point par Zacharias (1986). Il a été possible d’analyser les 99 échantillons en 7 jours en s’affranchissant d’enzymes fraîches de rumen de vaches remplacées par une solution de cellulase.


© J.L. Janeau

Figure 16. Bain marie pour l’incubation de tubes à essai renfermant l’herbe broyée et une solution de cellulase pour opérer la digestion de l’herbe.

IV. Les relations plante-eau et l'isotopie

Le laboratoire du BEEH de l'UKZN dispose d'un équipement récent, le « *DLT 100 Liquid Water Isotope Analyser* » pour analyser les isotopes de l'eau. Grace à l'encadrement de Simon Lorentz et David Ward, il a été possible d'étudier les relations acacias-eau dans le contexte de l'invasion d'arbres. Cette étude a également bénéficié des conseils de Thierry Bariac, spécialiste des isotopes de l'eau à Bioemco-Grignon. Pour déterminer les profondeurs de prélèvement d'eau par les arbres, il est nécessaire de prélever des échantillons de sol et de sève d'arbres, d'en extraire l'eau et d'analyser cette eau. L'extraction d'eau des échantillons repose sur une méthode de distillation sous vide qu'il n'était pas possible d'envisager au Cap, où l'équipement existe, dans les délais de cette étude. C'est sous la supervision et l'encadrement de Patricia Richard au laboratoire Bioemco de Grignon, sous la responsabilité de Thierry Bariac, que nous avons pu extraire l'eau des échantillons de sol et de sève par distillation sous vide pendant trois semaines et ensuite analyser les isotopes de l'eau par spectroscopie de masse.

La distillation sous vide est un processus simple mais qui nécessite un appareillage complexe (Fig. 17). Les échantillons fermés hermétiquement et pesés sont gelés à l'azote liquide pour éviter toute évaporation lors de leur ouverture et positionnement dans la colonne de distillation. Une fois ouverts et positionnés (par série de 20 échantillons), ils sont mis sous vide et chauffés. L'eau s'évapore et vient se condenser dans des tubes refroidis à l'azote liquide en dehors du caisson chauffant (azote qu'il faut ajuster régulièrement). Une fois la distillation terminée, un pesage des échantillons et du liquide récolté permet de vérifier si la distillation a été totale. En effet, par évaporation du liquide, il y a concentration de l'eau non-évaporée en isotopes lourds. Si l'eau n'est pas extraite totalement, le rapport isotopique sera fortement modifié et les résultats biaisés. La durée de distillation est variable en fonction de la quantité d'eau à évaporer, du type de sol (notamment de sa capacité de rétention) et de la quantité de sol. La durée totale de distillation (montage, démontage, nettoyage) pour les carottes d'acacias pouvait être de 9 h en moyenne et plus ou moins 15 h pour les sols.

Les mesures isotopiques ont été complétées par des mesures de potentiels hydriques caractérisant l'état hydrique de la plante et notamment un stress hydrique. De jeunes feuilles d'acacias ont été sélectionnées et introduites une par une dans une bombe de Scholander (Scholander *et al.* 1965) (Fig. 18) sous la supervision de Jean-Louis Janeau et David Ward. Les mesures ont été faites avant le lever du jour lorsque les arbres présentent une transpiration minimale et au milieu du jour lorsque la transpiration est maximale.

© S. Grellier

Figure 17. Colonne de distillation au laboratoire INRA-Grignon d'une capacité de 20 échantillons. En haut, le bloc chauffant avec les échantillons et en bas les tubes de collecte d'eau refroidi à l'azote liquide.

© S. Grellier

© S. Grellier

Figure 18. Bombe de Scholander muni d'un manomètre à gauche et avec la sève sortant de la tige soumise à une forte pression (gaz azoté) à droite.

Chapitre 3. Evolution temporelle et spatiale des ravines et de la population d’*Acacia sieberiana*

Bassin versant de la communauté de Potshini (Afrique du Sud) en saison humide (février 2010) fortement érodé par de profondes ravines et dont les versants sont envahi par l’*A. sieberiana*.

Ce chapitre permet d'aborder le système étudié d'un point de vue spatial et temporel à l'échelle du paysage et sur le long terme. Il s'agit d'une première approche de l'invasion ligneuse et de l'érosion en ravine dans cette région semi-humide d'Afrique du Sud. Ce chapitre est divisé en trois parties. La première partie présente l'évolution du bassin versant au cours des 64 dernières années du point de vue de l'invasion ligneuse et de l'érosion en ravine. Il s'agit ici, à l'échelle du paysage, de déterminer les taux d'augmentation de densité des acacias et les taux d'avancement des ravines par l'analyse de photographies aériennes. Cette première partie est un préliminaire à l'étude de l'impact de l'invasion d'arbres sur l'érosion en ravine (chapitre 5).

A cette analyse spatiale et temporelle de la surface du bassin versant vue du ciel, succède une étude spatiale du sol et sous-sol par les approches géophysiques à l'échelle d'une toposéquence. Cette étude géophysique a permis de dresser des cartes du sol et du sous-sol, liées aux propriétés physiques et à la teneur en eau du sol et du sous-sol. Certaines données présentées dans cette deuxième partie seront donc utilisées dans la troisième partie pour étudier la répartition spatiale de la population *d'Acacia sieberiana* en fonction des propriétés du sol et du sous-sol.

I. Evolution des ravines et de l'invasion ligneuse sur les 64 dernières années

A 64 year study of gully extension and woody plant encroachment in a subhumid grassland of South Africa (first part)

Séraphine Grellier(1), Jaco Kemp(2), Nicolas Florsch(3), Jean-Louis Janeau(1), David Ward(4),
Sébastien Barot(5), Pascal Podwojewski(1), Simon Lorentz(6),
Christian Valentin(7)

[1] *IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology (BEEH), Rabie Saunders Building, UKZN, Box X01, Scottsville, 3209, South Africa*

[2] *Department of Geography & Environmental Studies, University of Stellenbosch, Private. Bag X1, Matieland, 7602, South Africa*

[3] *Université Pierre et Marie Curie IRD, UMI n°209 UMMISCO, 4 place Jussieu, 75005 Paris, France*

[4] *School of Biological and Conservation Sciences, John Bews Building, UKZN, Scottsville, 3209, South Africa*

[5] *IRD-BIOEMCO, Site Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05, France*

[6] *School of Bioresources Engineering and Environmental Hydrology (BEEH), Rabie Saunders Building, UKZN, Box X01, Scottsville, 3209, South Africa*

[7] *IRD-BIOEMCO, 32 av. H. Varagnat, 93143 Bondy cedex, France*

Keywords: *Acacia sieberiana, aerial photographs, erosion, piping, subsurface.*

This part constitutes the first part of an article submitted to Landscape Ecology in an adapted format along with some of the results presented in chapter 6.

Abstract

Gully erosion and woody plant encroachment are frequently observed in grasslands worldwide. Gully erosion driven by water processes is usually affected by topography, land-use change and vegetation cover. However, very few studies have simultaneously considered tree encroachment and gullies. We used aerial photographs to study *Acacia sieberiana* encroachment and gully erosion in a South African grassland (KwaZulu-Natal Province) for a period lasting 64 years. At the catchment scale, results showed that grassland was transformed into savanna in 35 years. *Acacia* tree canopy cover in the catchment reached a maximum of 9.45 % in 2009 indicating that encroachment may not stop yet. Gully area in the catchment increased by 3.9 % in the last 64 years and represented 12.76 % of catchment area in 2009. Mean estimated sediment loss was 200 Mg ha^{-1} y^{-1}, indicating a high erosion rate mainly due to swelling and shrinkage.

1. Introduction

Gully formation is a widespread natural erosion phenomenon that induces significant soil losses, with both ecological and economic consequences (Bull 1981; Lal 1998; Poesen et al 2003; Valentin et al 2005). Gullies are found in a large variety of landscapes, from arid desert areas to humid cultivated lands and grasslands. The factors controlling gully erosion are numerous including bedrock type, soil type, topography, soil surface features, vegetation cover associated with climatic conditions, especially rainfall intensity and alternation of wet and dry seasons (Imeson and Kwaad 1980; Poesen et al 2003). Anthropogenic factors include commonly land-use change (Ward et al 2001) and activities associated with road and construction sites as well as animal pathways (Valentin et al 2005).

The understanding of gully initiation (threshold determination) and gully evolution (driving factors) is still debated due to methodological advances (Vandekerckhove et al 2003; Martínez-Casasnovas 2003). Further research is needed, especially with regard to the ways in which environmental changes affect gully erosion (Poesen et al 2003). Previous studies often highlighted the importance of land-use changes associated with vegetation cover on processes affecting gully erosion (Vandekerckhove et al 2000; Ward et al 2001; Chaplot et al 2005; Muñoz-Robles et al 2010). High vegetation cover reduces runoff susceptibility (Böhm and Gerold 1995; Molina et al 2007; Podwojewski et al in press) by intercepting rainfall and limiting soil crusting (Podwojewski et al 2008). Lower runoff results in a lower concentration of water and flow sheer stress which in turn limits the formation of gullies (Poesen et al 2002).

Subhumid grasslands in KwaZulu-Natal province of South Africa, even with their high vegetation cover (herbaceous layer) relative to agricultural fields, present severe gully erosion (Sonneveld et al 2005). “Dongas” as these gullies locally called in South Africa are typical of the mountainous foothills of KwaZulu-Natal. Existing gullies were already present 1000 years ago (Botha 1994). Gullies are mainly controlled by intrinsic factors such as bedrock types, terrain morphology and bioclimatic zones (Botha 1996). The colluvial sediments accumulated in this region are very prone to erosion (Rienks et al 2000) and the hilly slopes and distribution of rainfall in the area (Yaalon 1987) have favored gully erosion.

Another phenomenon affecting grasslands worldwide is woody plant encroachment. Woody plant encroachment has been observed in grassland and savanna for approximately 150 years (Van Auken 2009).

The objective of this study constituting the first part of the article are to analyse the long term evolution of gully extension and woody plant encroachment over a period of 64 years in a subhumid grassland catchment of South-Africa using a time-series of aerial photographs.

2. Materials and methods

2.1 Study site

The study site is located in South Africa where both gully erosion and woody plant encroachment are severe, particularly in the KwaZulu-Natal province. For approximately 30 years, trees have been encroaching on savannas and subhumid grasslands in the area. The communal grassland of Potshini village, in the foothills of the Drakensberg mountains, 8km south of Bergville (28º 48' 37" S; 29º 21' 19" E), has been studied for 10 years (Fig. 1). It is representative of the upper part of the Thukela river basin with a 30,000 km² catchment. We focused our research on a 2.5 km^2 sub-catchment of the grassland (from 1 217 m altitude to 1 452 m) which presents wide and deep gullies and tree encroachment.

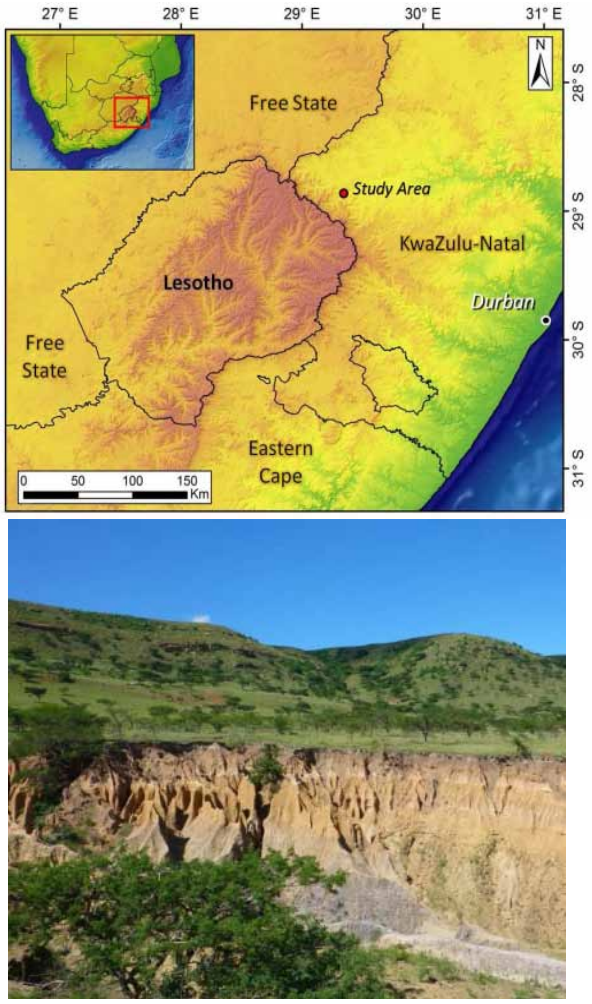


Figure 1. Localization of the study site at the top and a photograph of gully and encroachment in the catchment at the bottom.

The climate of this area is characterized as subtropical subhumid with summer rainfall. The mean annual precipitation is on average 754.4 mm for the last 65 years. The average annual temperature is 13 ºC (Schulze et al 1997). This site is classified as grassland biome by Mucina and Rutherford (2006). The specific biome is the “Northern KwaZulu-Natal moist grassland” usually dominated by *Themeda triandra* and *Hyparrhenia hirta* (Mucina and Rutherford 2006). The encroaching trees, *Acacia sieberiana* var. *woodii* (Burtt Davy) Keay & Brenan, are indigenous. The geology of the site is characterized by fine-grained sandstones, shales, siltstone and mudstones of the Beaufort and Ecca Groups of the Karoo Supergroup that alternate in horizontal successions (King 2002). Unconsolidated colluvial deposits from Pleistocene fill the valleys and are very prone to linear gully erosion (Botha 1994). Soil types are Acrisols upstream and Luvisol downstream (W.R.B. 1998) with two main soil horizons: a 40 cm thick A horizon and a B horizon generally occurring between 40 to 90 cm depth. The topsoil is cohesive with dark grayish brown color (10YR 4/1 to 10YR 4/3) and 20% clay, many fine and medium roots and with evidences of strong biological activity (termites, dung beetles, earthworms, etc.). Horizon B (Bt) is darker and very cohesive and hard. Clay, mainly illite, accumulates in this B horizon up to 50%. Soils are not sodic but present pipe systems first reported by Henkel et al (1938).

2.2 Data collection and processing

Monthly rainfall was obtained for a period lasting from 1940 until 2002 at the Bergville weather station (South African Weather Service) located 8km north of the catchment. Rainfall was collected between 2003 and 2009 at the weather station of the Potshini catchment.

A set of four non-georeferenced aerial photos with scale of 1/20 000 was obtained from the National Geospatial Information (NGI), Department of Land Affairs, South Africa. The dates for the image sets were 1945, 1962, 1976 and 1985. A more recent view of the area (May 2009) was obtained from a series of digital airborne images collected using a small, low speed, remotely-controlled unmanned aerial vehicle (UAV) called *Pixy* (Asseline et al 1999). The digital camera used was a Canon EOS450D with a focal length of 34 mm to cover the area with 18 images. The images were taken from an altitude of 150 m. This flight altitude and focal length yielded a spatial resolution of 10 cm. Two orthorectified aerial photographs from 2001 and 2006 with pixel resolutions of 2.7 m were obtained from NGI to complete the dataset and provide image sets from seven different dates (1945, 1962, 1976, 1986, 2001, 2006 and 2009).

Orthorectification was performed on all non-georeferenced photographs as well as the 2009 photographs using ArcGis 9.3 (ESRI 2008). The 2006 orthorectified image was used as a reference for orthorectification because it was the most spatially and radiometrically accurate. A maximum of identified points (between 53 and 113 for the 4 non-georeferenced photographs) such as fence corners and rocks were used to optimize the accuracy of orthorectification. The 18 images from the 2009 Pixy survey were orthorectified using 400 DGPS points surveyed in the field during image capture. These points were highly visible features that could be identified on the imagery, and were surveyed with an overall accuracy of ±5cm. Between 20 and 50 control points per image were used, and a spline transformation method was used to optimize orthorectification (Bangamwabo 2009).

Digitizing of different features was done manually. Gully contours and trees with their canopies were digitized for each photograph. A shapefile was created with the different layers matching the different features for each of the studied years. Increase of the gully area was calculated for six time-periods: 1945-1961, 1962-1975, 1976-1984, 1985-2000, 2001-2005, 2006-2009 for the whole gully system by calculating the difference in the digitized gully areas for each year.

3. Results

3.1 Woody plant encroachment over 64 years at the catchment scale

A. sieberiana has been present in significant numbers in the grassland since about 1985 (Fig. 2). In 1945, the first year of the study, the area showed nearly no trees (Fig. 2A). Trees started really encroaching from the north (lower part) and south (upper part) of the catchment in 1985 (Fig. 2B). In 2009, trees were located everywhere except in a small area on the eastern part of the catchment that is still free of trees (Fig. 2C).

The occupation area of trees increased during the study period from 1945 to 2009 when it reached 9.45% of the catchment area (Fig. 3). This increase followed the same trend as large tree density as they represent the largest portion of woody cover area. Large trees represented 8.73 % of the catchment area in 2009. In comparison, medium trees occupied 0.71 % of the catchment area in 2006 (Table 1). This year was the peak year of encroachment with a maximum density of trees (27.85 trees ha^{-1}). The density of large trees still increased in 2009 while the density of medium and small trees decreased mostly because they grew into medium and large trees (Fig. 3).

The mean average rainfall for each period showed an increase from 1945 to 2009 going from 752 mm y^{-1} to 906 mm y^{-1}. Considering each period (n=6), a positive correlation between mean rainfall and tree canopy area was found (R^2= 0.81, p = 0.014).

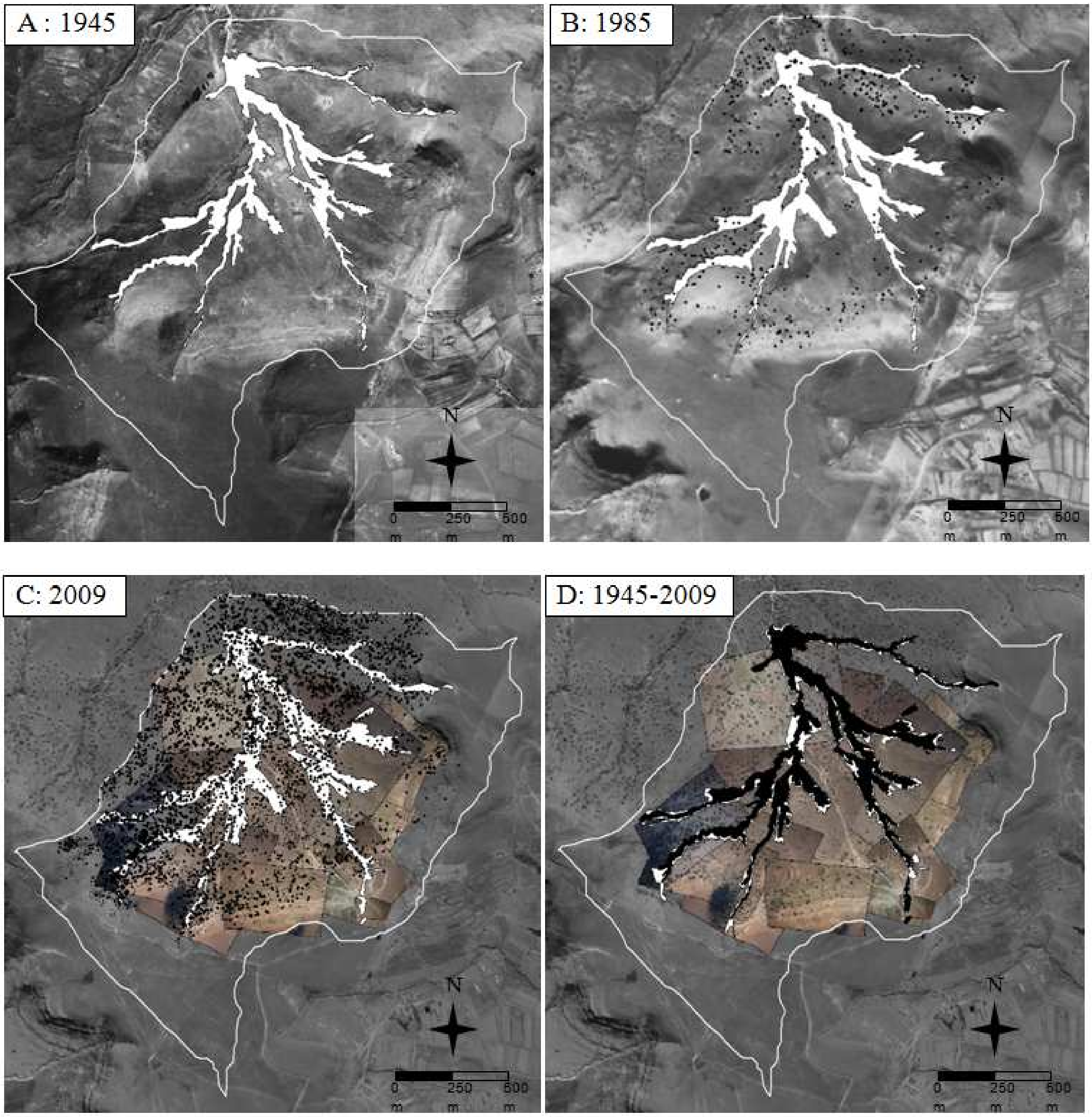


Figure 2. Aerial view of gullies (in white) and trees (small black points) in Potshini catchment in 1945, 1985 and 2009. Last picture D shows in white the extension of gullies between 1945 and 2009.

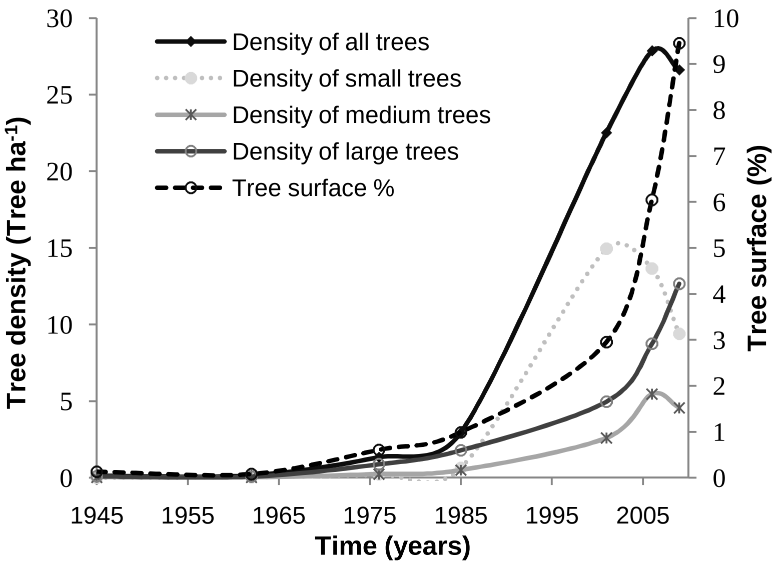


Figure 3. Tree density and tree surface in the catchment from 1945 to 2009. Small trees (canopy area < 1 m^2), medium trees (1 m^2< canopy area< 15 m^2), large trees (canopy area> 15 m^2).

Table 1. Percentage of canopy area of all trees, small trees (<1 m^2 canopy area), Medium trees (between 1 m^2 and 15 m^2 canopy area) and large trees (>15 m^2 canopy area).

Years	All trees	Small trees	Medium trees	Large trees
1945	0.13	0.00	0.00	0.13
1962	0.08	0.00	0.00	0.08
1976	0.60	0.00	0.03	0.58
1985	0.99	0.00	0.06	0.93
2001	2.95	0.01	0.71	2.23
2006	6.04	0.01	0.93	5.11
2009	9.45	0.01	0.71	8.73

3.2 Gully extension rate over 64 years at the catchment scale

From 1945 to 1975, gully retreat area remained constant at a value of 950 m^2 y^{-1} (Fig. 4). Between 1976 and 1984, gully retreat area increased up to 2300 m^2 y^{-1} and stayed stable until 2001. A second increase was observed in the period 2001-2005 and reached 4000 m^2 y^{-1}. Finally, in 2009, gully retreat area continued increasing at 4441 m^2 y^{-1}. Since 1945, 3.9 % of the grazing surface of the catchment was lost through gully erosion. Significant correlation was found between rainfall and gully retreat area (R^2= 0.67, p = 0.04).

To compare our results with other studies, we converted retreat area (m^2 y^{-1}) into Mg of sediment per hectare of gully surface per year (Martínez -Casanovas 2003) or gully erosion rate. The estimation of sediment produced by gullies has been computed assuming an average bank gully height of 3 m (field observations), a bulk density of 1.4 g cm^{-3} which was the mean across three soil profiles in the catchment from 0 to 120 cm and a total gully surface of 31.9 ha in the study site in 2009. The estimated total retreat area between 1945 and 2009 was 1 531 m^2 y^{-1}, which gives a mean of 200 Mg ha^{-1} y^{-1}.

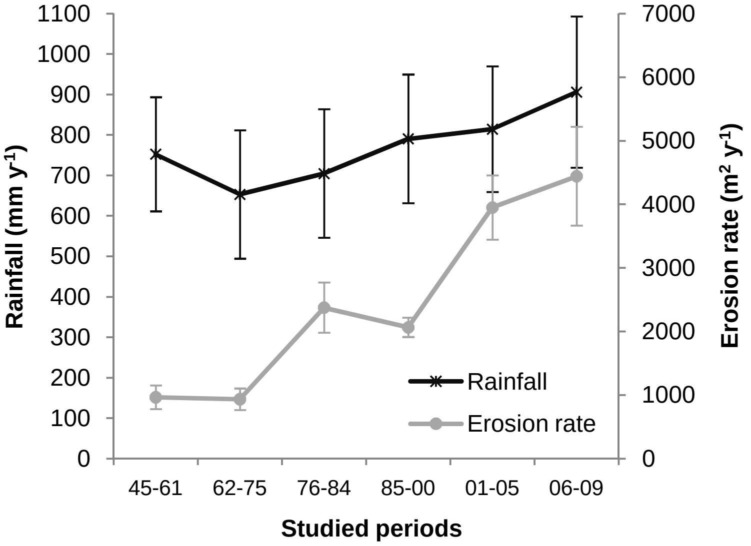


Figure 4. Mean annual rainfall and erosion rates of the whole gully system during the six studied periods: 1945-1961, 1962-1975, 1976-1984, 1985-2000, 2001-2005, 2006-2009. Vertical bars represent standard deviation for rainfall and the error on the digitalization for erosion rate.

4. Discussion

4.1 Woody plant encroachment evolution at the catchment scale over 64 years

At the catchment scale, tree canopy area has increased by 10-fold in 35 years if we consider that the increase started in 1976. Prior to 1976, the percentage tree cover was very low. The encroachment rate found in this study is in the range of worldwide studies but is in the lower range (Table 2). The values of encroachment rate in the different cited studies are rarely above 1 % y^{-1}. The only case reported over 1 % y^{-1} matched to an area already encroached at the beginning of the study and where large trees able to reproduce can accelerate the encroachment. If we only refer to the % of tree canopy area, the studied grassland has still a large potential for encroachment with only 9.45 % of area covered by trees in 2009. Even if a slight decrease of total density is observed in the last few years (from 2006), the population is probably not yet at equilibrium as the large tree density still increases and these large trees are the biggest seeds producers. After 2006, inter-tree competition may have taken place as well as changes in other disturbances factors such as herbivory and fires (Sankaran et al 2005; Ward 2005), which can modify tree population. Unfortunately we have very few data about these factors during the study period to relate them to the tree cover increase.

Few studies (Goslee et al 2003) indicated that encroachment was not correlated with rainfall, but many others (Ansley et al 2001; Sankaran et al 2005; Widenmaier and Strong 2010) indicated that rainfall was an important factor of tree population in grassland. Rainfall played an important role in this subhumid system but is probably not the sole cause of expansion of *Acacia sieberiana* in our study site. Cattle density has increased as well as human population in the last few years (pers. comm. from Potshini community). The local human population uses trees as fuel, which would limit encroachment by tree cutting, while cattle should increase encroachment through seeds spreading in the grassland (Van Auken 2009).

Table 2. Comparison of tree encroachment rates (ER) in grasslands or savannas in the world.

AUTHORS' NAME	LOCATION	STUDY PERIOD	ER (% y^{-1})	COMMENTARIES
Coop and Givnish 2007	Caldera Valley New Mexico, USA	1935-1996	0.3	
Robinson et al 2008	Pilbara, Western Australia	1943-2001	0.4	
Goslee et al 2003	Southern New Mexico	1936-1996	0.7	
Archer et al 1988	South Texas	1941-1983	0.5	
Ansley et al 2001	South Western USA	1976-1995	2.2	untreated area
Ansley et al 2001	South Western USA	1976-1995	1.1	tree cleared area in 1976
Roques et al 2001	Swaziland	1947-1990	0.7	
Hudak and Wessman 2001	Madikwe, South Africa	1955-1996	0.7	
Wigley et al 2009	Hlabisa (Hluhluwe), South Africa	1937-2000	1.0	
Laliberte et al 2004	Southern New Mexico	1937-2003	0.2	
This study	Drakensberg foothills, South Africa	1945-2009	0.27	Considering encroachment starting in 1976

4.2 Gully extension at the catchment scale over 64 years

The high gully extension rate of 200 Mg ha^{-1} y^{-1} found for this area is in the range of badlands in France (Bufalo and Nahon 1992; Descroix and Olivry 2002) or of badlands in the Barasona reservoir basin in Spain with 302–455 Mg ha^{-1} y^{-1} (Martínez -Casasnovas and Poch 1998). However, our estimated rate is much higher than those of many studies referenced in Poesen et al (2003) where rates ranged from 0.1 to 64.9 Mg ha^{-1} y^{-1}. This rate was also very high compared to the estimate given by Chaplot et al (in press) of 4.8 Mg ha^{-1} y^{-1} at our study site but at a smaller scale (1 m width bank gully) and for a short time period of 45 min during one rainfall simulation. Chaplot et al (in press) showed that 62 % of total soil loss was due to runoff, 24 % to splash erosion and only 13 % to collapse of aggregates from gully bank. This last process may however play a more important role in gully erosion of this area. Three months after rainfall simulation, an important part of the 1 m-wide gully bank collapsed (pers. obs.), which was mainly due to swelling and shrinkage of clay. Over 64 years, loss of similar entire blocks may have often occurred after heavy rains. The large difference between the erosion rates calculated over the short term (4.8 Mg ha^{-1} y^{-1}) and over the long term (200 Mg ha^{-1} y^{-1}) demonstrates the importance of bank erosion due to swelling and shrinkage processes in the gully erosion of this area (De Ploey 1974). This high erosion rate does not actually reflect the soil loss exported from the catchment to an outlet reservoir because of deposition in such deep and large gullies (Imeson and Kwaad 1980; Rieke-Zapp and Nichols in press). Once the gully bank fall in pieces at the bottom of the gully, the surface exposed to rainfall is high and not covered by vegetation. Removal and deposition of sediment downstream is thus easier (Podwojewski et al in press) as observed in rehabilitated zones filled by sediment inside the gullies.

Humid regions usually have higher rates of gully retreat than arid regions (Poesen et al 2003; Samani et al 2010). This is consistent with the significant correlation found in this study between rainfall and gully retreat area. Gully erosion increases significantly with rainfall >40 mm day^{-1} (Bouchnak et al 2009), or >25 mm hr^{-1} (Rieke-Zapp and Nichols in press).

5. Conclusions

This study confirms that erosion processes and mechanisms depend on the spatial and temporal scale of the study. At the small temporal scale (one rainy season or one rainfall simulation), or at the small spatial scale (the plot scale, often studied), processes linked to rill and gully erosion are mostly observed as surface processes: splash detachment, soil surface crusting and runoff depending mostly on rainfall characteristics and vegetation cover. At a larger scale (space and time), other processes can be observed such as swelling and shrinkage of gully bank that are highly variable in space and time.

Rainfall increased over the years as well as gully erosion and woody plant encroachment indicating that rainfall may be one of the factors influencing both processes.

However, a more focused study is necessary to identify the link between woody plant encroachment and gully erosion. This study will be presented in chapter 5 and constitute the second part of this article which has been submitted to Landscape Ecology.

6. Acknowledgments

The authors would like to thank the University of KwaZulu-Natal, the Institute of Research and Development (IRD), for infrastructure and financial support. We further thank the community of Potshini for sharing their land and participating to the experiment, especially Sibonelo Mabaso. A special thank go to Jean Asseline and Jean-Louis Rajot for their “pixy” experience.

7. References

Ansley RJ, Ben WX, Kramp BA (2001) Observation: long-term increases in mesquite canopy cover in a North Texas savanna. Journal of Range Management 54:171-176

Archer S, Scifres CJ, Bassham CR et al (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:11-127

Asseline J, Noni GD, Chaume R (1999) Note sur la conception et l'utilisation d'un drone lent pour la télédétection rapprochée. Photo Interprétation 37:3-9

Bangamwabo VM (2009) Spatial and temporal extent of land degradation in a communal landscape of KwaZulu-Natal, South Africa. Unpubl. MSc. Thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa

Böhm P, Gerold G (1995) Pedo-hydrological and sediment responses to simulated rainfall on soils of the Konya Uplands, Turkey. Catena 25:63-75

Botha GA (1996) The geology and palaeopedology of late quaternary colluvial sediments in northern Kwazulu/Natal. Council for Geoscience, Pretoria, South Africa

Botha GA, Wintle AG, Vogel JC (1994) Episodic late Quaternary palaeogully erosion in northern KwaZulu-Natal, South Africa. Catena 23:327-340

Bouchnak H, Felfoul MS, Boussema MR et al (2009) Slope and rainfall effects on the volume of sediment yield by gully erosion in the Souar lithologic formation (Tunisia). Catena 78:170-177

Bufalo M, Nahon D (1992) Erosional processes of Mediterranean badlands: a new erosivity index for predicting sediment yield from gully erosion. Geoderma 52:133-147

Bull WB (1981) Soils, geology, and hydrology of deserts. In: Evans DD, Thames JL (eds) Water in desert ecosystems. Dowden, Hutchinson and Ross, Stroudsberg, Pennsylvania, pp 42–58

Chaplot V, Giboire G, Marchand P et al (2005) Dynamic modelling for linear erosion initiation and development under climate and land-use changes in northern Laos. Catena 63:318-328

Chaplot V, Brown J, Dlamini P et al (in Press) Rainfall simulation to identify the storm-scale mechanisms of gully bank retreat. Agricultural Water Management

Coop JD, Givnish TJ (2007) Spatial and temporal patterns of recent orest encroachment in montane grasslands of the Valles Caldera, New Mexico, USA. Journal of Biogeography 34:914-927

De Ploey J (1974) Mechanical properties of hillslopes and their relation to gullying in Central semi-arid Tunisia. Zeitschrift-Geomorphologie 21:177-190

Descroix L, Olivry JC (2002) Spatial and temporal factors of hydric erosion in black marls badlands of the French southern Alps. Hydrological Sciences Journal 47:227-242

ESRI (2008) ArcGIS 9.3, ArcMap-ArcEditor Environmental Systems Research Institute, Inc. New-York, USA

Goslee SC, Havstad KM, Peters DPC et al (2003) High-resolution images reveal rate and pattern of shrub encroachment over six decades in New Mexico, U.S.A. Journal of Arid Environments 54:755-767

Henkel JS, Bayer AW, Coutts JRH (1938) Subsurface erosion on a Natal midlands farm. South African Journal of Science 35:236-243

Hudak AT, Wessman CA (2001) Textural analysis of high resolution imagery to quantify bush encroachment in Madikwe Game Reserve, South Africa, 1955–1996. International Journal of Remote Sensing 22:2731-2740

Imeson AC, Kwaad FJPM (1980) Gully types and gully prediction. K.N.A.G. Geografisch Tijdschrift XIV 5:430-441

King GM (2002) An explanation of the 1:500 000 general hydrogeological map. Department of Water Affairs and Forestry, Pretoria, South Africa

Lal R (1998) Soil erosion impact on agronomic productivity and environment quality. Critical Review Plant Science 17:319-464

Laliberte AS, Rango A, Havstad KM et al (2004) Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. Remote Sensing of Environment 93:198-210

Martínez-Casasnovas JA (2003) A spatial information technology approach for the mapping and quantification of gully erosion. Catena 50:293-308

Martínez-Casasnovas JA, Poch RM (1998) Estado de conservación de los suelos de la cuenca del embalse Joaquín Costa. Limnetica 14:83-91

Molina A, Govers G, Vanacker V et al (2007) Runoff generation in a degraded Andean ecosystem: Interaction of vegetation cover and land use. Catena 71:357-370

Mucina L, Rutherford MC (eds) (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa

Muñoz-Robles C, Reid N, Frazier P et al (2010) Factors related to gully erosion in woody encroachment in south-eastern Australia. Catena 83:148-157

Podwojewski P, Janeau JL, Grellier S et al (in Press) Influence of grass soil cover on water runoff and soil detachment under rainfall simulation in a sub-humid South African degraded rangeland. Earth Surface Processes and Landforms doi: 10.1002/esp.2121

Poesen J, Vandekerckhove L, Nachtergaele J, Oostwoud Wijdenes D, Verstraeten G, van Wesemael B (2002) Gully erosion in dryland environments. In: Bull LJ, Kirkby MJ (eds.) (2002) Dryland rivers: hydrology and geomorphology of semi-arid channels. Wiley, Chichester, UK pp. 229–262

Poesen J, Nachtergaele J, Verstraeten G et al (2003) Gully erosion and environmental change: importance and research needs. Catena 50:91-133

Rieke-Zapp DH, Nichols MH (in press) Headcut retreat in a semiarid watershed in the southeastern United States since 1935. Catena

Rienks SM, Botha GA, Hughes JC (2000) Some physical and chemical properties of sediments exposed in a gully (donga) in northern KwaZulu-Natal, South Africa and their relationship to the erodibility of the colluvial layers. Catena 39:11-31

Robinson TP, van Klinken RD, Metternicht G (2008) Spatial and temporal rates and patterns of mesquite (*Prosopis* species) invasion in Western Australia. Journal of Arid Environments 72:175-188

Roques KG, O’Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280

Samani AN, Ahmadi H, Mohammadi A et al (2010) Factors controlling gully advancement and models evaluation (Hableh Rood Basin, Iran). Water Resources Management 24:1531-1549

Sankaran M, Hanan NP, Scholes RJ et al (2005) Determinants of woody cover in African savannas. Nature 438:846-849

Schulze RE (eds) (1997) South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria, South Africa

Sonneveld MPW, Everson TM, Veldkamp A (2005) Multi-scale analysis of soil erosion dynamics in KwaZulu-Natal, South Africa. Land Degradation & Development 16:287–301

Valentin C, Poesen J, Li Y (2005) Gully erosion: impacts, factors and control. Catena 63:132–153

Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931-2942

Vandekerckhove L, Poesen J, Wijdenes DO et al (2000) Characteristics and controlling factors of bank gullies in two semi-arid mediterranean environments. Geomorphology 33:37-58

Vandekerckhove L, Poesen J, Govers G (2003) Medium-term gully headcut retreat rates in Southeast Spain determined from aerial photographs and ground measurements. Catena 50:329-352

Ward D (2005) Do we understand the causes of bush encroachment in African savannas? African Journal of Range & Forage Science 22:101-105

Ward D, Feldman K, Avni Y (2001) The effects of loess erosion on soil nutrients, plant diversity and plant quality in Negev desert wadis. Journal of Arid Environments 48:461-473

W.R.B (1998) World Reference Base for Soil Resources. n°84 World Soil Resources Reports, FAO, Rome

Widenmaier KJ, Strong WL (2010) Tree and forest encroachment into fescue grasslands on the Cypress Hills plateau, southeast Alberta, Canada. Forest Ecology and Management 259:1870-1879

Wigley BJ, Bond WJ, Hoffman MT (2009) Bush encroachment under three contrasting land-use practices in a mesic South African savanna. African Journal of Ecology 47:62–70

Yaalon DH (1987) Is gullying associated with highly sodic colluvium? Further comment to the environmental interpretation of southern African dongas. Palaeogeography, Palaeoclimatology, Palaeoecology 58:121-123

II. Etude des compartiments de subsurface par la géophysique

Study of subsurface soil layers by geophysics

Séraphine Grellier(1), Nicolas Florsch(2), Jean-Louis Janeau(1), Pascal Podwojewski(1),
Christian Camerlynck(2), Simon Lorentz(3)

[1]IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa
[2]Université Pierre et Marie Curie, UMI n°209 UMMISCO, 4 place Jussieu, 75005 Paris, France
[3]School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa

Keywords: bedrock, catena, duplex soil, electrical conductivity, electromagnetic

Some of the data presented here are used in an article in preparation (cf. Appendixes 5 and 6).

1. Introduction

Investigation of subsurface layers is of great interest to better understand the relation between trees, soil properties and subsurface water (Robinson et al., 2008). Traditional local point measurements by digging pits is usually time consuming, expensive, destructive and not well adapted to the landscape scale (Buchanan and Triantafilis 2009; Tromp-van Meerveld and McDonnell 2009). Geophysical methods are non-destructive approaches that can be used to investigate subsurface layers of soil (Soupios et al., 2007; Robinson et al., 2008).

Geophysics, by measuring soil electrical conductivity (EC) (or its reciprocal, resistivity) provides useful information on physical and chemical properties of soil (Lesch and Corwin 2003). EC is directly linked to soil salinity, clay content, cation exchange capacity (CEC), clay mineralogy, soil pore size and distribution, and soil moisture (McNeill 1992). For non-saline soil, Corwin and Lesch (2005) reported that EC mainly depends on soil texture, moisture content, bulk density, and CEC.

Depending on the method used, different soil depths of investigation are possible (Vannaroni et al., 2004). The classical electrical resistivity survey and the vertical electrical soundings (VES) are based on continuous current ("CC") and determine the resistivity distribution of the sounded soil volume. Practically, a continuous electric current is sent into the ground using buried electrodes and the resulting potential differences are measured (Samouëlian et al., 2005). The range of possible depth of investigation is considerable (Michot et al., 2003; Soupios et al., 2007) and depends on the spacing chosen between current (emitting) electrodes and potential (receiving) electrodes.

Electromagnetic methods based on induction are also very promising to study soil properties and soil moisture and have been specially developed for this aim over the last few years (Robinson et al., 2007; Hossain et al., 2010). These methods measure EC of the soil by emitting magnetic fields from a powered coil. A receiver measures the secondary magnetic field produced by the currents induced by the first emission. One of these electromagnetic methods is the time-domain electromagnetic method (TDEM) which can investigate soil depths from 3 m to 100 m (Vannaroni et al., 2004). Frequently used electromagnetic methods are the EM31 and EM38, among others. These slingram methods investigate shallow depths. EM38 investigates near subsurface soil layers from 0 m to 1.5 m while EM31 investigates slightly deeper depths from 1.5 to 4 m. These methods are complementary and can be used together to obtain better understanding of soil subsurface properties (Vannaroni et al., 2004; Triantafilis and Monteiro Santos 2010).

EM38 and EM31 are especially appropriate for the current study through their shallow investigation depth which is the depth where most tree and/or grass roots are found (Schenk and Jackson 2002). Both instruments can be easily manipulated on a landscape scale to obtain data for large areas. Many studies have related the electrical conductivity measured with EM38 and/ or EM31 with soil properties and soil moisture (Sherlock and McDonnell 2003; Reedy and Scanlon 2003; Brevik et al., 2006; Robinson et al., 2008; Abdu et al., 2008;

Tromp-van Meerveld and McDonnell 2009; Hossain et al., 2010). However, the earlier studies did not dissociate layers with very different properties from the near subsurface i.e. 0-1.5 m. In the case of duplex soils, two layers are superimposed in this interval and involve different properties (Chittleborough 1992) which will drive water processes within the soil (Gregory et al., 1992) and thus influence the presence and abundance of tree and grass roots (Dracup et al., 1992; Macinnis et al., 2010). The chemical and physical properties of duplex soils may change over time (Fitzpatrick et al., 2000) which often increases their susceptibility to water erosion (Cox and Pitman 2002). Some studies determined the depth of aquifers (Schumann et al., 2003; Buchanan et al., 2009), or provided the spatial distribution of soil properties with depth (Triantafilis and Santos 2010), and/or determined the depth of the interface between two distinct layers (Sudduth et al., 2010) by using electromagnetic methods. However, it is still a methodological challenge to obtain EC of a first layer and a second layer and their interface depth by measurement with EM38. Moreover, there are few studies involving the new EM38-MK2 equipment that simultaneously measure two distinct depth ranges.

Here, we conduct a preliminary investigation of the soil subsurface at the landscape scale with EM31, TDEM and VES methods to understand the global properties of a duplex soil. Then, to relate soil properties to tree spatial patterns (*cf*. part III of this chapter) a more detailed survey is presented at the plot scale (1.5 ha) with EM38-MK2 and EM31 devices.

2. Materials and methods

2.1 Site description

Experiments have been conducted in a grassland of KwaZulu-Natal, South Africa (28º 48' 37" S; 29º 21' 19" E, 1300 m), where tree encroachment started 35 years ago (Grellier et al., submitted). The climate is subhumid subtropical with a rainy summer (October–April) and a mean annual precipitation of 745 mm over the last 65 years. The mean annual temperature is 13 °C (Schulze 1997) and potential evaporation is between 1600 mm and 2000 mm per year (Guy and Smith 1995). The geology is represented by fine-grained sandstones, shales, siltstone and mudstones of the Beaufort and Ecca Groups of the Karoo Supergroup (Permien) which alternate in horizontal successions (King 2002). Unconsolidated colluvial deposits from the Pleistocene fill the valleys and are very prone to gully erosion (Botha 1994). These colluvial deposits are intruded by 1-8 m wide dykes of dolerite from the Jurassic (Mucina and Rutherford 2006). The duplex soils are classified into luvisols (World Reference Base 1998) with two well-delimited main horizons. The A horizon is coherent with brown color (10YR 4/1 to 10YR 4/3) with more sand and silt, with many fine and medium roots. The Bt Horizon (up to 50% of clay) is dark brown, very coherent and hard with a coarse blocky structure (details of chemical and physical analyses are given in Appendix 1).

2.2 Geophysical methods

2.2.1 Time domain electro-magnetic method (TDEM)

The TDEM sounding method is based on the following: a horizontal current wire loop emits an EM impulse in the space. It produces “eddy” currents which spread deeper and deeper in the ground and also expand and decline in amplitude. Those currents produce a secondary magnetic field that is detected in a secondary coil or the same coil as the transmitter (Fig. 1).

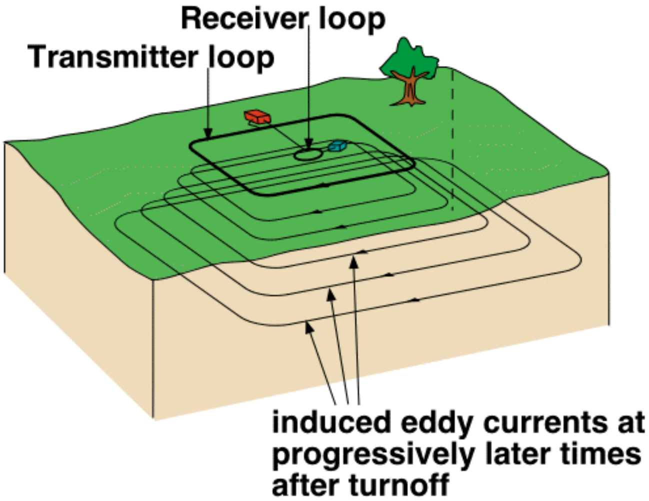


Figure 1. Schematic representation of the TDEM method (http://www.ncwater.org/Education_and_Technical_Assistance/Ground_Water/TDEM/).

The measured parameter is the secondary magnetic field (the primary magnetic field has been shut down). The longer the measurement, the deeper the recovered signal. If we use one circular loop of radius (a) and a current I over a homogeneous half space of resistivity ρ , the secondary magnetic field time (B_z) variation as measured in the same loop is given by:

$$\frac{\partial B_z}{\partial t} \cong -\frac{I\rho^{-\frac{3}{2}}\mu_0^{\frac{5}{2}}a^2}{20\sqrt{\pi}}t^{-\frac{5}{2}}$$

where t is the time and μ_0 is the magnetic permeability.

The apparent resistivity (ρ_a) is obtained by inverting this formula as a function of time (t):

$$\rho_a = \left(\frac{Ia^2}{20\,\partial B_z/\partial t}\right)^{\frac{1}{2}} \frac{\mu_0^{\frac{5}{3}}}{\pi^{\frac{1}{3}}} t^{-\frac{5}{2}}.$$

2.2.2 Vertical Electrical Sounding (VES)

The VES consists of sending electrical currents into the ground by using two current electrodes C1 and C2 and by measuring the resulting voltage between two receiving electrodes named P1 and P2[1]. Various protocols are used, having relative advantages and disadvantages. We used the traditional "Wenner $-\alpha$" array: the four electrodes are equi-spaced by a distance (a) and lined up (Fig. 2).

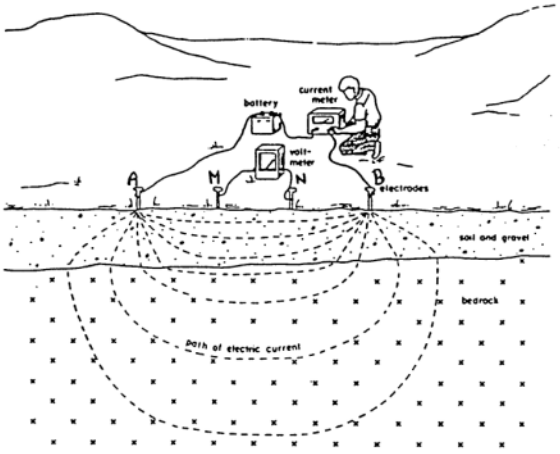


Figure 2. Disposition of electrodes for the Wenner protocol used in this study (Source: www.argenco.ulg.ac.be/GEO3_Hydrogeologie/pdf/These_Rentier/14_AnnexeB.pdf)

A formula can be used to calculate the resistivity ρ of the soil from the current I (into C1 and C2) and the difference of potential ΔV (between P1 and P2) measured in the field. We define the apparent resistivity by the expression:

$$\rho_a = K\frac{\Delta V}{I}$$

where K is the geometric coefficient and varies according to the kind of array used (here Wenner $K = 2\pi a$, with *a* being the spacing between the electrodes). The apparent

---

[1] C for current and P for potential. The French tradition calls A and B for the current and M and N for the potential.

resistivity is also the resistivity of a hypothetically homogeneous medium that would lead to the same ratio $\frac{\Delta V}{I}$. By increasing the electrode spacing, the investigation depth gets deeper and deeper; we can calculate the apparent resistivity of thicker and deeper layers. Soil homogeneity and "tabular structure" (resistivity is only a function of the depth due to the single dimension of the method) are generally assumed to be correct to interpret the data.

2.2.3 EM31 and EM38-MK2 electromagnetic methods

The EM31 and EM38-MK2 electromagnetic methods are inductive methods. One coil serves as a transmitter and produces an alternative magnetic field in the ground (9.8 kHz for the EM31 and 14.6 kHz for the EM38-MK2). As a first approximation, this magnetic field induces an electric field in the ground as stated by the Maxwell equation:

$\vec{\nabla} \times \vec{E} = -\frac{\partial \vec{B}}{\partial t}$ where $\vec{E}$ is the electric field and $\vec{B}$ the magnetic induction.

The induced electric field leads to a density current $\vec{J} = \sigma \vec{E}$ where σ is the conductivity (they are often named "eddy currents" due to the rotational pattern). These currents produce a secondary magnetic field which is detected by the receiving coil and in fact is stacked with the primary field caused by the transmitter. Hence the secondary field reflects the conductivity. The depth of investigation mainly depends on the coils separation, but also depends on the direction of the coils' axes. In the Geonics devices that we used, the coils were maintained at the same height above the ground, and two modes were used: the vertical dipole mode in which the two coil axes are vertical, and the horizontal mode where the axes are horizontal. EM31 (3.66 m long) investigates depths between 1 m and 4 m with a peak of sensitivity at 1.5 m. EM38-MK2 (where two spacings are simultaneously available: 1 m and 0.5 m) investigates depth between the surface and 1.5 m maximum, with a peak of sensitivity at 0.4 m in vertical mode and for the first 20 cm in horizontal mode (this is used more or less for the 1 m spacing and these depths are divided by a factor 2 for the 50 cm spacing).

During preliminary pit logging of resistivity (Appendix 4), we observed that two shallow layers could be distinguished by their large differences in resistivity; the first layer being more resistive and the second layer much more conductive. To determinate the conductivity of the first layer (σ_1) and the second layer (σ_2) with EM38-MK2, as well as the depth of the interface between both layers (Fig. 3), we developed a methodology detailed in Appendix 5. To summarize, two spacings with both the horizontal and vertical modes provided four independent measurements. Using four measurements allowed retrieval of the three parameters of a two-layer shallow subsurface, viz. the two conductivities and the depth of the interface. Bayesian inverse computation was used to obtain the three parameters (Appendixes 5 and 6). Comparison with other measurements by electrical sounding and methylene blue method of clay property determination validated this non-destructive approach (Appendix 6).

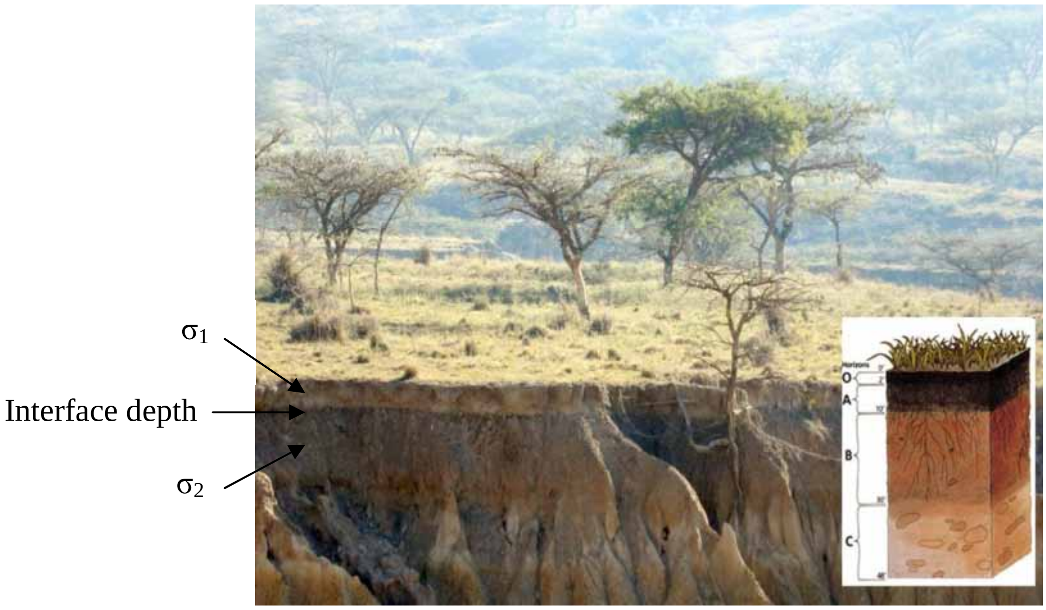


Figure 3. View of a gully bank with apparent two layers and their interface. Adapted from Wikipedia diagram (http://soils.usda.gov/education/resources/lessons/profile/profile.jpg).

As EM31 has a peak of sensitivity at 1.5 m depth, the row EC measured by EM31 could be directly used to obtain a map integrating EC values from about 1-4 m depth. When inverting the EM38-MK2 data, the interface depth between the two layers were between 75 cm and 85 cm, which follow the results of the diagraphy but did not fit with the traditional soil science methods separating A and B horizons at 40-50 cm depth. The transition given by geophysics is based on the inflexion point of the amount of mineralogical clays (highly conductive material) while soil science relies mainly on soil colors, structure and texture. According to the several previous field measurements and the pit logging we consider Fig. 4 as a representative EC profile of the study site.

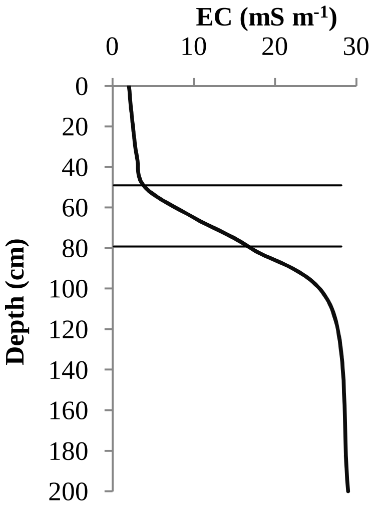


Figure 4. Schematic representation of electrical conductivity (EC) of a typical soil profile of the study area.

Observations following soil science criteria allow the determination of the beginning of the transition around 50 cm (separation of A and B horizons), while geophysics indicates the inflexion of the transition to be about 80 cm. As our goal is to correlate spatial pattern of trees with soil properties and especially soil moisture, we thus chose to determine EC for 0-0.5 m matching to the A horizon where important mechanisms may happen for young trees (Grellier et al., in prep.). We also determined EC for 0.5-1.5 m and as well 0.8-1.5 m to test if the transition zone had an impact on the correlation with trees.

2.3 Experimental design

In order to investigate the relationships between acacias and soil properties, we worked at several different spatial scales. We first covered an area of 15 ha along a catena from the upper part of the catchment to the lower part (Fig. 5A). To obtain a more detailed map of the subsurface layers which will be linked to spatial pattern of the acacias (*cf*. Part III), we then focused on a particular area of 100*150 m located downstream on the colluvial deposit at the head of the gully where acacias of all sizes were present (Fig. 5B). This plot is relatively flat with a mean slope of 6 ± 1.5 °.

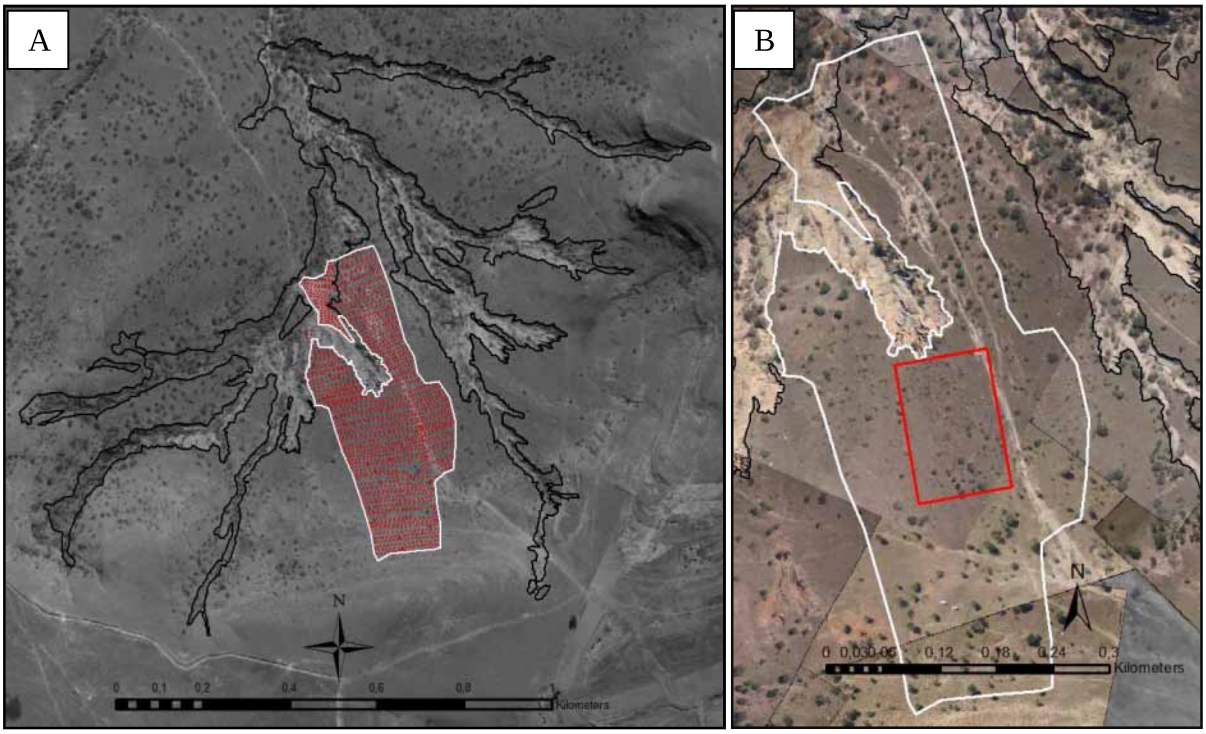


Figure 5. A) Delimitation of the catena area (15 ha) and tracks (GPS position) of the points measured by EM31 in June 2008. B) Focusing in the catena area (white line) and the plot scale area (red line) at the head of the gully head.

Catena scale 15 ha: We mapped EC of the catena area in June 2008 (dry season) with EM31 (Fig. 6). A GPS (Global Positioning System) fixed on the EM31 allowed us to follow parallel lines spaced by 10 m (Fig. 5A). VES and TDEM soundings were operated on this catena following a straight line from the upper part to the lower part every 50 m (represented by triangles on Fig. 6) to investigate the deeper subsurface compartments. Finally, single VES were conducted on different chosen points (extreme values of conductivity measured by EM31) in the catena area of 15 ha as shown on Fig. 6.

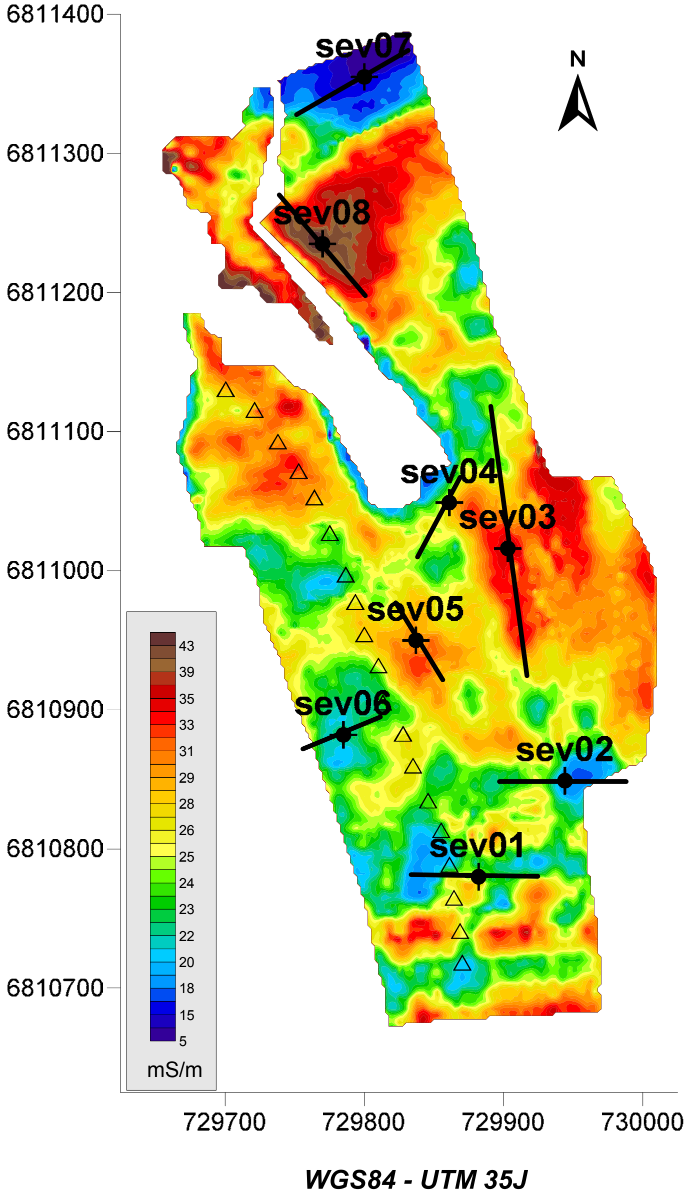


Figure 6. Conductivity (mS m^{-1}) of the subsurface layers (2 to 4 m depth) measured with EM31 in the catena area (15 ha). Location of single VES (SEV01 to SEV08) and VES and TDEM soundings made on the catena (triangles) are displayed on the map.

Plot scale (1.5 ha): On the 100*150 m plot shown in Fig. 5B, surveys were done in the wet and the dry seasons with EM31 and EM38-MK2. We followed a precise mesh and a gridding of 5*5 m. The calibration method was carefully operated in order to limit drift of the devices, especially for EM38-MK2 and is described in Appendix 5. All metals that could influence the devices were removed from the operator (such as sun glasses, reinforced shoes and cellphone) as well as all metallic structures located on the field for other experiments (such as fence and metallic tags on trees). Kriging was used as an interpolation method to obtain all maps of EC.

The relationship between EC and soil properties can be described by the formula given by Frohlich and Parke (1989) related to Archie's law:

$$\sigma_0 = \frac{1}{a} \times \sigma_{water} \times \Theta^k + \sigma_{surface}$$

where σ_0 is the bulk conductivity of clayey material, a is a factor reflecting the influence of mineral grains on current flow, σ_{water} is the conductivity of pore water, Θ is the volumetric water content, $\sigma_{surface}$ is the conductivity given by the surface of clay. The parameter k is defined as

$$\Theta^k = S_w{}^n \times \Phi^m$$

where S_w is the saturation degree, Φ is the porosity of the soil and m a material constant depending on the geometry of the pores, the compaction, the mineral composition and the insolating properties of cementation.

This formula actually represents a term linked to clayey properties and a term linked to water content. Soil properties of the clayey material that are included in $\sigma_{surface}$, a and k, do not change between two seasons. The dry season in the study area is characterized by very dry soil. Thus, measures of EC in dry season depend mainly on clay properties while in the wet season, water content is a significant factor influencing EC. Dry season EC should thus be highly positively correlated with $\sigma_{surface}$ and the following formula could be used to determine the volumetric clay content (Rhoades et al., 1989):

$$\sigma_{surface} = 2.3 \times C - 0.021$$

where $\sigma_{surface}$ is the EC of clay surface (mS cm^{-1}) and C is the volumetric clay content.

By calculating the difference between EC in the dry and wet seasons, it is possible to obtain values that are directly correlated with circulating soil water (Abdu et al., 2008). This pre-supposes that one follows a strict calibration procedure for the EM38-MK2 measurements and measures the same points for the two surveys to allow direct comparisons.

Logistic constraints prevented us from calibrating all measurements to obtain an absolute clay content map and absolute soil moisture map.

3. Results and discussion

3.1 Catena scale

3.1.1 TDEM soundings

TDEM investigates the deep subsurface layers. Different resistant bodies are shown in Fig. 7. The orange to red colouring is relative to resistant rocks (100 to 200 Ω.m) while the blue to green parts correspond to clayey and/or wet rocks between 10 and approximately 50 Ω.m. Close to the top (1350 m) and in the middle (1310 m) of the catena, shallow resistant bodies are observed (Fig. 7). They could either match to dolerite dikes or consolidating sandstone banks outcropping alternatly with less resistant mudstone or siltstone layers. One of the main features shown here is the resistant structure in the lower part of the catena (right side), where the contrast with the other part is significant. This resistive structure is probably also sandstone bedrock that is observed in the bottom of the downstream gullies and that cannot be eroded. The extension of vertical gully erosion is limited by this hard bedrock.

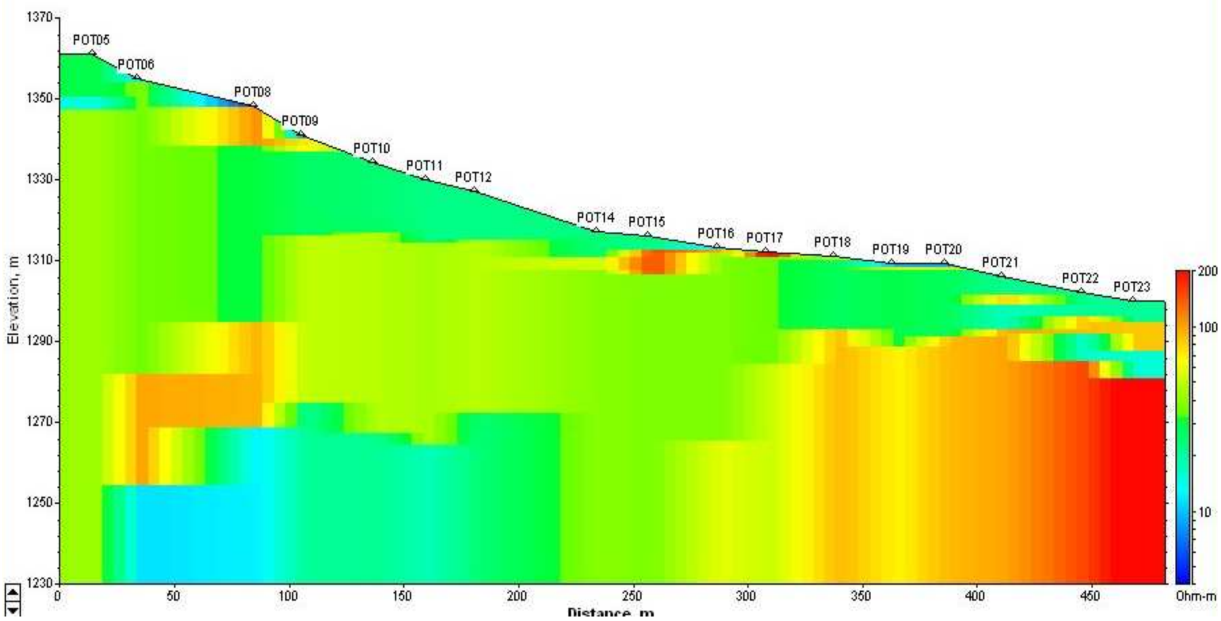


Figure 7. TDEM soundings results in the catena. Resistivity is represented with high values in red and lower values in blue.

3.1.2 EM31

The conductivities obtained with EM31 lay between 5 and 50 mS m^{-1}, with most values fell between 20 and 40 mS m^{-1} (Fig. 6). We can interpret the map as follows:

- Resistive parts (in blue) are the more consolidated rocks with less water or less clay;
- Conductive parts (in red) probably involve a higher amount of water up to the depth of investigation of the EM31 (up to 4 m), or a higher amount of clay.

The southern part of the catena (upper part) alternates between highly conductive layers (oriented East-West) in red and resistive layers in blue which are probably linked to the alternation of rock types; hard sandstones and softer mudstone or siltstone layers alternate at the top of the catena due to topographic effect.

At the northern part of the map there is a significant boundary between highly conductive material and less conductive material < 10 mS m^{-1}. This is probably due to a lateral geological change. We noticed a topographic depression at the boundary, associated with many dolerite rocks on the ground surface. A vertical dolerite dike may be located at this boundary and is high enough to create a wall stopping water flowing downstream where conductivity is the highest. Dolerite may appear relatively conductive or resistive depending on the water it contains.

Globally the conductivity was higher in the North (downstream part) and in the middle area than in the South where the slope is greater. This is due to accumulation of water in the downstream area. The heterogeneity between high and low conductivity in these areas is probably due to heterogeneity of bedrock types and associated water content. The strip along the gully is only due to instrument sensitivity due to the lack of soil at the gully cliff.

3.1.3 VES

The first VES called SEV01 was done in a transition zone in the upper part of the catena (Fig. 6) where the tabular hypothesis may not be correct. However, it provided a first insight of the subsurface. SEV01 showed a first resistive layer of almost 200 Ω.m and of 50 cm thickness (Fig. 8). This layer matches probably to the A horizon which dries the quickest in the dry season due to direct evaporation (close to the surface) and due to vegetation water uptake. Under this first layer there was a very conductive layer. Equivalence analysis showed that the parameters of this layer can be between 8 Ω.m with 30 cm thickness and 20 Ω.m with 90 cm thickness (respectively according to equivalence laws). It is reasonable to accept a mean value of 12 Ω.m with approximately 50 cm thickness. This layer is more humid and more clayey than the first layer and may match the B horizon where clay accumulates. Beneath this second layer, the equivalence analysis gives a third more resistive layer of 50 Ω.m. Thereafter, layers becomes more and more resistive with increasing depth perhaps because of the decrease of the weathering of the bedrock.

SEV02 and SEV06 were located on resistive patches (Fig. 6). SEV06 had a conductive layer at 5 m depth which causes the general decay of the resistivity curve (Fig. 9); however this measurement is at the detection limit depth of the EM31 which explains the resistive value given by this analysis. This conductive horizon may be interpreted as a residual water sheet overlying a less permeable layer. Above, the vadose zone (between the surface and 5 m) is relatively dry, indicating that good drainage may induce higher resistivity. The “apparent” bedrock is at about 10 m depth. There was an inconsistent result regarding the deep conductive layer resistivity value.

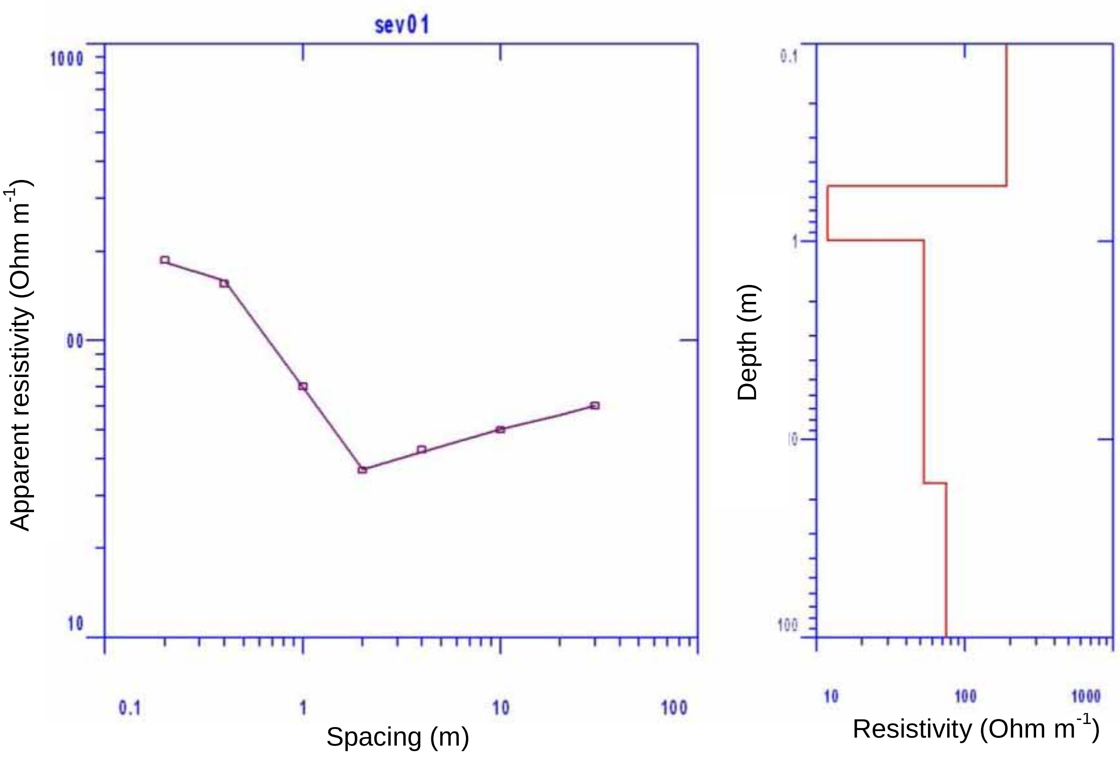


Figure 8. Results of the SEV01 (left) and the equivalence analysis (right) giving the depth of the possible layers and their resistivity.

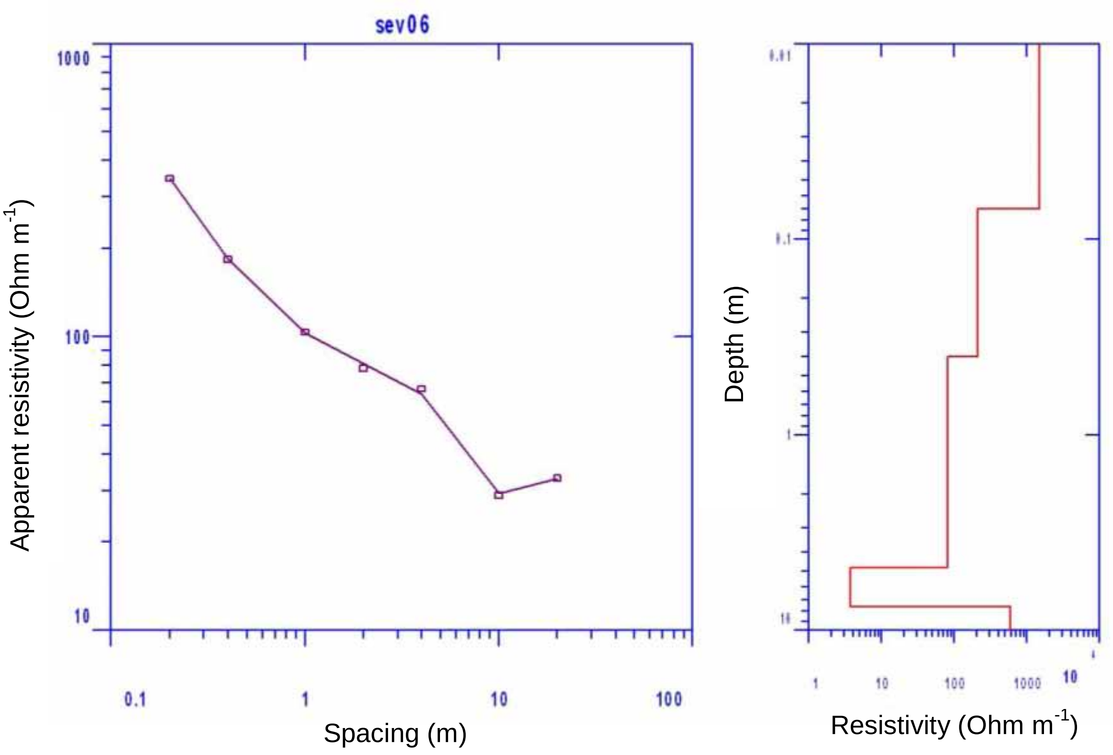


Figure 9. Results of the SEV06 (left) and the equivalence analysis (right) giving the depth of the possible layers and their resistivity.

Two solutions were found differing only for the deep layer. Both were of an equal quality when looking at the fit, but one presents a deep conductive layer at 2.1 Ω.m with 6.4 m thickness and the other at 11.4 $\Omega \cdot \text{m}$ with 13.2 m thickness. However, in the first case the recomputed EM31 conductivity is about 40 mS m^{-1}, while in the second case it was 26 mS m^{-1}, which is much closer to the value found with the EM31 at this point (about 20 mS m^{-1}). Hence the second interpretation is more realistic. A layer of 2.1 Ω.m is a salty layer, while 11.4 Ω.m is probably a clayey and very wet (saturated) zone (of course we cannot exclude the possibility that there is some salt present). Moreover the interpretation of thickness also depends on the appropriateness of the interpretation.

SEV02 was more complex and allows several solutions. The fit with the EM31 conductivity value measured at that point (18-20 mS m^{-1}) suggests the following solution: a shallow resistive layer is found at the surface with 377 Ω.m and 20 cm thickness. Then, until 4 m depth, there is another resistive layer but at 70 Ω.m. At 4 m there was a less resistant layer (as SEV06) with 29 Ω.m, which is probably very permeable, before reaching the bedrock.

SEV05 and SEV03 surveys were made in conductive patches (Fig. 6). SEV05 was very robust, with a first resistive layer at 305 Ω.m and a thickness of 30 cm, probably the A horizon, then a layer of 11.6 m thickness at 30 Ω.m matches the B horizon and finally a 90 Ω.m bedrock below. SEV03 sounding allowed several equivalent interpretations which can be sorted by comparing EM31 conductivity value (34 mS m^{-1}) with the one found for each solution. The first layer was close to 440 Ω.m and 19 cm thickness. The second layer was at 30 Ω.m with 2.35 m followed by a conductive layer at 16 Ω.m with a 4.3 m thickness, before reaching the bedrock.

SEV4 was located close to the gully and near a large acacia tree. This VES is interesting because it is expected to be well-drained by the acacia. Here we recorded 0.33 m of resistant soil, then almost 2 m at 54 Ω.m and then a 35 Ω.m layer with a 12.5 m thickness. The last layer was > 80 Ω.m. This VES was similar to SEV03.

To summarize, VES on the catena gave the following results:

- In all cases, a first resistant soil layer (more than 100 Ω.m) was found of variable thickness.
- Either this first layer was directly followed by a conductive layer or an additional but less resistant layer may exist;
- Three profiles showed a more conductive layer at 2 m or 5 m in depth;
- Almost all profiles indicated a bedrock around 80-90 Ω.m but at variable depths;
- Heterogeneity of subsurface resistivity was clear, indicating high variability of subsurface properties. This is in agreement with the EM31 results between 1.5 and 4 m that shows also heterogeneity in the catena due to 1) topographic effects and alternation of sandstones and

mudstones or siltstones in the upper part of the catchment, and 2) the spatial heterogeneity of the colluvial layer in the downstream part of the catchment.

3.2 Plot scale

EC of the first layer (0-0.5 m) had low conductive values between 0 and 11 mS m^{-1} for the wet season (Fig. 10). In the dry season the soil was even less conductive, with maximal values at 7 mS m^{-1} which may be an aberrant point due to its single value. Thus the difference between wet and dry season was low and stayed mainly between -2 and 3 which was included in the error range of the EM38-MK2 device (2 mS m^{-1}). However, the southeastern part of the area showed higher soil moisture in wet season.

The second layer integrating the transition zone (0.5-1.5 m) was more conductive than the first layer, with values ranging between 4 and 44 mS m^{-1}. Different areas appeared on the map with the eastern/north-eastern part being the most conductive for both the wet and the dry seasons. Differences between the two seasons were much higher than for the first layer with a circulation of water in the south-western part of the area in the wet season while on the north-eastern part there was higher soil moisture in the dry season.

A similar layer excluding the transition area (0.8-1.5 m) had higher conductivity with a similar pattern to that explained above. The difference between the two seasons was also more clearly marked with the same trends as for the 0.5-1.5 m layer.

Finally, the EM31 gave EC with values between 20 and 38 mS m^{-1} for 1-4 m depths. The wet and the dry seasons had similar values. There were three distinct areas on the map in the wet and the dry seasons: 1) the north-eastern part was very conductive, as we also observed in the upper layer (0.5-1.5 m), 2) the central part of the area was less conductive, and 3) the south-western part where EC was high. The difference between the wet and the dry seasons was very low with most values between -2 and 3 similar to the first layer. At this depth, there was an increase in soil moisture in the wet season in the north-eastern part of the area.

These results indicate that seasonal soil moisture increased especially at 0.5-1.5 m depths. In the surface layer and below 1.5 m, seasonal variation of soil moisture was very low. This can be explained by the presence of the B horizon with higher clay amounts. Water arriving at the soil surface in the first layer either directly evaporates (high temperatures in February induce high evaporation), is transpired by the herbaceous layer (that uses water specifically during the growth period, in February) or percolates deeper (Ward et al., 2001). Water is halted in the B horizon due to clay properties capable of retaining water. Soil water saturation may allow water to percolate deeper but this is only seen during very high rainfall events. The field trip in February was preceded by a few days without rain and thus the soil was not at saturation.

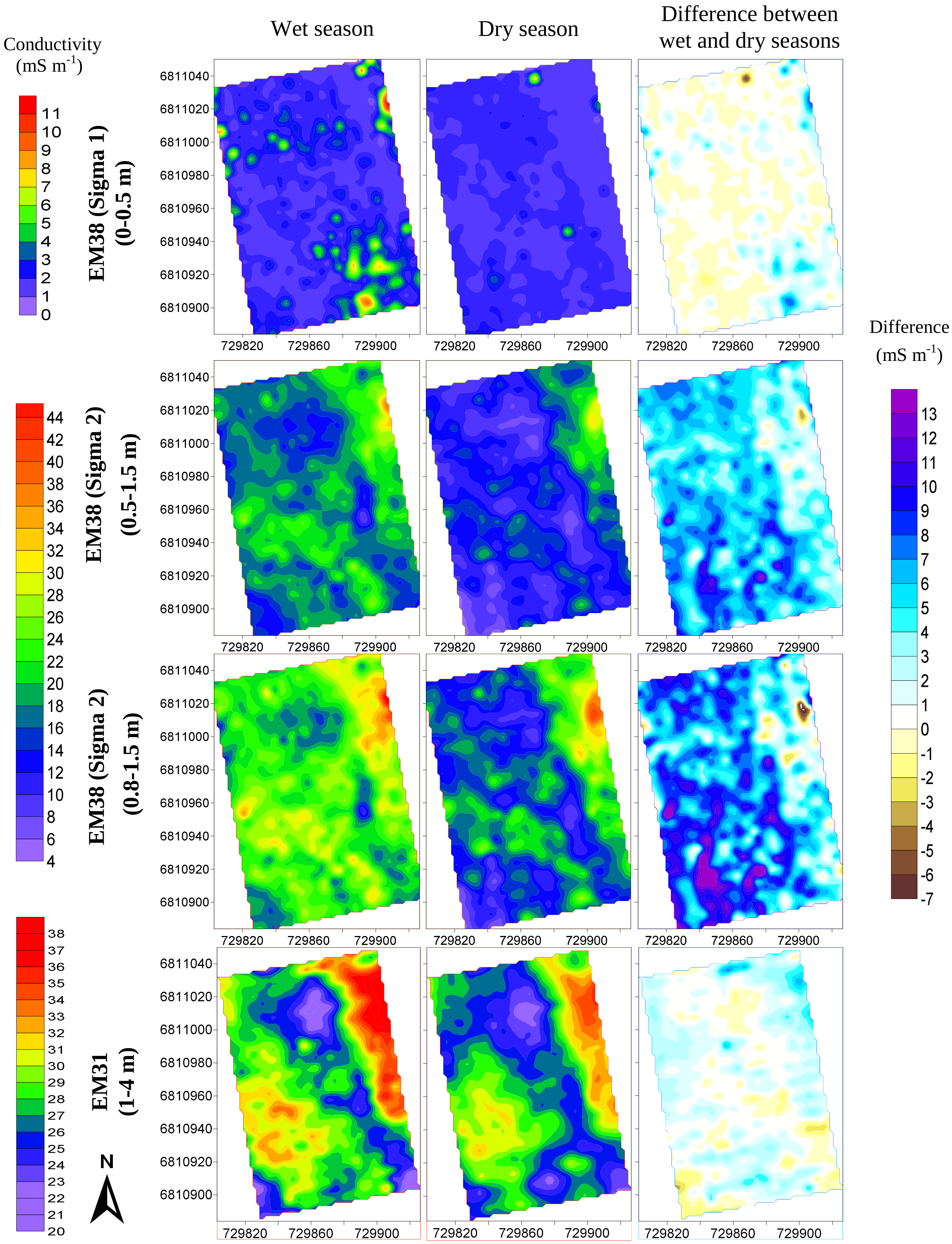


Figure 10. Conductivity (mS m^{-1}) of the 1.5 ha area for four horizons (0-0.5 m, 0.5-1.5 m, 0.8-1.5 m and 1-4 m) investigated by EM38-MK2 and EM31 in the dry and wet seasons. The last column of figures is the difference in conductivity between the wet and dry seasons with a color scale displayed on the right of the figure. X and Y axes are the coordinates in UTM 35J.

In the study area, seasonal soil moisture was not homogeneously distributed. The north-eastern part had higher soil moisture in the dry season than in the wet season. This is unusual but can be explained by the very high clay content (highest EC in the dry season). This very clayey zone is not very permeable to water and may promote water logging at its surface (Cox and McFarlane 1995). In February, it was apparently not yet moist. After the frequent rains of March and April of 2010, deep drainage may finally wet the soil layer which then resulted in very high retention properties and remained moist until (at least) June that year. In such very clayey areas, soil moisture is often not available for plants due to the high retention capabilities. Contrastringly, the south-western part of the area had intermediate clay content and became more humid in the wet season.

The geophysical investigation performed in this study provided information on the deep subsurface characteristics of the grassland, with a heterogeneous pattern due to different combination of geological events. It is however in the first 4 m below the surface that trees may be most affected. The association of EM31 and EM38-MK2 results with specific Bayesian methods allowed for successful mapping of electrical conductivity at the catena scale for three identified layers from the surface to 4 m below the surface. Hydrologically active water (seasonal soil moisture) was mainly located in the second layer (0.5-1.5 m) and will be used in the next section for determination of correlations with the spatial pattern of acacias.

4. References

Abdu, H., D. A. Robinson, M. Seyfried, and S. B. Jones. 2008. Geophysical imaging of watershed subsurface patterns and prediction of soil texture and water holding capacity. Water Resources Research 44:W00D18.

Brevik, E. C., T. E. Fenton, and A. Lazari. 2006. Soil electrical conductivity as a function of soil water content and implications for soil mapping. Precision Agriculture 7:393-404.

Buchanan, S., and J. Triantafilis. 2009. Mapping water table depth using geophysical and environmental variables. Ground Water 47:80-96.

Chittleborough, D. J. 1992. Formation and pedology of duplex soils. Australian Journal of Experimental Agriculture 32:815-825.

Corwin, D. L., and S. M. Lesch. 2005. Apparent soil electrical conductivity measurements in agriculture. Computers and Electronics in Agriculture 46:11-43.

Cox, J. W., and D. J. McFarlane. 1995. The causes of waterlogging in shallow soils and their drainage in southwestern Australia. Journal of Hydrology 167:175-194.

Cox, J., and A. Pitman. 2002. Catchment scale water and soil balance modelling in southern Australia. 12th ISCO Conference, Beijing.

Dracup, M., R. K. Belford, and P. J. Gregory. 1992. Constraints to root-growth of wheat and lupin crops in duplex soils. Australian Journal of Experimental Agriculture 32:947-961.

Fitzpatrick, R. W., R. H. Merry, and J. W. Cox. 2000. What are saline soils and what happens when they are drained? Journal of the Australian Association of Natural Resource Management June:26-30.

Frohlich, R. K., and C. D. Parke. 1989. The electrical resistivity of the vadose zone — field survey. Ground Water 27:524-530.

Gregory, P. J., D. Tennant, A. P. Hamplin, and J. Eastham. 1992. Components of the water-balance on duplex soils in western Australia. Australian Journal of Experimental Agriculture 32:845-855.

Grellier S, Kemp J, Florsch N, Janeau J-L, Ward D, Barot S, Podwojewski P, Lorentz S, Valentin C. A 64 year study of gully extension and woody plant encroachment in a subhumid grassland of South Africa. *Landscape Ecology*: Submitted.

Guy, R. M., and J. M. B. Smith. 1995. A land potential classification for KwaZulu-Natal. Unpubl. N/A/95/12, KwaZulu-Natal Department of Agriculture, Cedara, South Africa.

Hossain, M. B., D. W. Lamb, P. V. Lockwood, and P. Frazier. 2010. EM38 for volumetric soil water content estimation in the root-zone of deep vertosol soils. Computers and Electronics in Agriculture 74:100-109.

King, G. M. 2002. An explanation of the 1:500 000 general hydrogeological map. Department of Water Affairs and Forestry, Pretoria, South Africa.

Lesch, S. M., and D. L. Corwin. 2003. Using the dual-pathway parallel conductance model to determine how different soil properties influence conductivity survey data. Agronomy Journal 95:365-379.

Macinnis-Ng, C. M. O., S. Fuentes, A. P. O’Grady, A. R. Palmer, D. Taylor, R. J. Whitley, I. Yunusa, M. J. B. Zeppel, and D. Eamus. 2010. Root biomass distribution and soil properties of an open woodland on a duplex soil. Plant and Soil 327:377-388.

McNeill, J. D. 1992. Rapid, accurate mapping of soil salinity by electromagnetic ground conductivity meters. In: advances in measurement of soil physical properties: bringing theory into practice, Specific Publication 30, Soil Science Society of America, Madison, Wisconsin:209-229.

Michot, D., Y. Benderitter, A. Dorigny, B. Nicoullaud, D. King, A. Tabbagh. 2003. Spatial and temporal monitoring of soil water content with an irrigated corn crop cover using surface electrical resistivity tomography. Water Resources Research 39:1138.

Mucina, L., and M. C. Rutherford. 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa.

Reedy, R. C., and B. R. Scanlon. 2003. Soil water content monitoring using electromagnetic induction. Journal of Geotechnical and Geoenvironmental Engineering 129:1028–1039.

Robinson, D. A., C. S. Campbell, J. W. Hopmans, B. K. Hornbuckle, S. B. Jones, R. Knight, F. Ogden, J. Selker, and O. Wendroth. 2007. Soil moisture measurement for ecological and hydrological watershed-scale observatories: a review. Vadose Zone Journal 7:358-389.

Robinson, D. A., H. Abdu, S. B. Jones, M. Seyfried, I. Lebron, and R. Knight. 2008. Eco-geophysical imaging of watershed-scale soil patterns links with plant community spatial patterns. Vadose Zone Journal 7:1132-1138.

Samouëlian, A., I. Cousin, A. Tabbagh, A. Bruand, and G. Richard. 2005. Electrical resistivity survey in soil science: a review. Soil & Tillage Research 83:173-193.

Schenk, H. J., and R. B. Jackson. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology 90:480-494.

Schulze, R. E. 1997. South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria, South Africa.

Schumann, A. W., and Q. U. Zaman. 2003. Mapping water table depth by electromagnetic induction. Applied Engineering in Agriculture 19:675-688.

Sherlock, M. D., and J. J. McDonnell. 2003. A new tool for hillslope hydrologists: spatially distributed groundwater level and soil water content measured using electromagnetic induction. Hydrological Processes 17:1965–1977.

Soupios, P. M., M. Kouli, F. Vallianatos, A. Vafidis, and G. Stavroulakis. 2007. Estimation of aquifer hydraulic parameters from surficial geophysical methods: A case study of Keritis Basin in Chania (Crete – Greece). Journal of Hydrology 338:122-131.

Sudduth, K. A., N. R. Kitchen, D. B. Myers, and S. T. Drummond. 2010. Mapping depth to argillic soil horizons using apparent electrical conductivity. Journal of Environmental and Engineering Geophysics 15:135-146.

Triantafilis, J., and F. M. Santos. 2010. Resolving the true electrical conductivity using EM38 and EM31 and a laterally constrained inversion model. In: 19th world congress of soil science, soil solutions for a changing world, 1-6 August, Brisbane, Australia.

Tromp-van Meerveld, H. J., and J. J. McDonnell. 2009. Assessment of multi-frequency electromagnetic induction for determining soil moisture patterns at the hillslope scale. Journal of Hydrology 368:56-67.

Vannaroni, G., Pettinelli, E., Ottonello, C., Cereti, A., Monica, G. D., Vento, D. D., Lellis, A. M. D., Maio, R. D., Filippini, R., Galli, A., Menghini, A., Orosei, R., Orsini, S., Pagnan, S., Paolucci, F., Pisani, A. R., Schettini, G., Storini, M., & Tacconic, G. 2004. MUSES: multi-sensor soil electromagnetic sounding. Planetary and Space Science 52:67-78.

W.R.B. 1998. World reference base for soil resources. 84, World Soil Resources Reports, FAO, Rome.

Ward, P. R., and F. X. Dunin. 2001. Growing season evapotranspiration from duplex soils in south-western Australia. Agricultural Water Management 50:141-159.

III. Importance des propriétés du sol sur la répartition spatiale des acacias

Spatial relationships between acacias, soil moisture and soil properties in encroached grassland of South Africa

Séraphine Grellier(1), Nicolas Florsch(2), Jean-Louis Janeau(1), Pascal Podwojewski(1), Christian Camerlynck(2), Sébastien Barot(3), David Ward(4), Simon Lorentz(5)

[1]*IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa*
[2]*Université Pierre et Marie Curie, UMMISCO, 4 place Jussieu, 75005 Paris, France*
[3]*IRD-BIOEMCO, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France*
[4]*School of Biological & Conservation Sciences, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa*
[5]*School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa*

Keywords: *Acacia sieberiana,* clay, EM38, EM31, geophysics, season, soil horizon

Article in preparation for submission to Vadose Zone Journal.

1. Introduction

The causes of woody plant encroachment in grassland have been widely studied (Archer et al. 1995; Jeltsch et al. 1996; Brown and Archer 1999; Higgins et al. 2000; Sankaran et al. 2004; Briggs et al. 2005; Sankaran et al. 2005; Kraaij and Ward 2006; Meyer et al. 2007; Gignoux et al. 2009; Riginos 2009; Van Auken et al. 2009; Grellier et al. submitted). Scientists have only recently started to explore the factors that control the structure and spatial pattern of encroaching tree populations (Wiegand et al. 2006; Robinson et al. 2010; Halpern et al. 2010) which should give new insights on this complex problem that is not yet fully understood (Ward 2005; Graz 2008). Various models have been proposed, including spatially explicit models (Wiegand et al. 2005; 2006) where trees are aggregated in patches whose dynamics is driven mainly by rainfall and inter-tree competition with a shift between facilitation and competition (Callaway and Walker 1997; Halpern et al. 2010). Soil nutrient patches have also been highlighted as driving spatial patterns of palm trees in tropical humid savanna of Lamto (Barot et al. 1999). If other studies mentioned the importance of soil properties on dynamics of woody vegetation (Britz and Ward 2007; Schleicher et al. 2011), few have tested the effects of soil properties on vegetation spatial pattern in grasslands (Browning et al. 2008; Eggemeyer and Schwinning 2009; Robinson et al. 2010, Trinogga 2010).

The reasons for the lack of studies are linked with the technical issues of measuring soil properties at the landscape scale, which is the most relevant scale to analyze these processes. The recent interdisciplinary links between soil science, hydrology and ecology (Young et al. 2010) offer useful possibilities for throwing new light on the issue by taking into account more factors that could be missed otherwise. Within this concept, Robinson et al. (2008) associated geophysics methods for mapping soil properties at the watershed scale and vegetation spatial patterns. The same authors also presented a study on tree-grass co-existence where they showed that conductivity, related to soil properties were lower under trees (oak) than under grass cover, indicating that trees were located on soils with lower clay content (Robinson et al. 2010).

The application of geophysics to ecology and especially to studying spatial vegetation patterns needs more attention. Indeed, soil properties and soil moisture are two linked factors that could influence tree establishment and growth. The two layer hypothesis of Walter (1971) distinguishes the near subsurface soil layer where most grass roots grow (Snyman 2009; Kambatuku et al. 2011) and deeper layers where tree roots are mainly found. These two layers could increase competition for water as tree roots mostly access deeper water that has not been used by grass and has percolated through the soil. This suggests that trees could depend, at least in some savannas, on the capacity of water to reach deeper soil layers. However, soil moisture content depends on more complex hydrological processes than described by Walter, especially on duplex soils with two distinct layers (Chittleborough 1992). Water fluxes influenced by hydrology and trees (Nadezhdina et al. 2010) are not only vertical, from the surface to deeper layers, but can also be lateral (Lin 2006) as well as vertical but from deeper to shallower layers (e.g. Ludwig et al. 2003). Moreover, soil moisture depends on soil texture and other soil properties (that may vary at the landscape scale) and landscape characteristics (Robinson et al. 2007). Thus, the identification of different soil properties depending on depth could influence tree spatial pattern in grasslands and savannas (Breshears et al. 2009).

In this study we explore the relationships between spatial pattern of trees and soil properties such as clay content and soil moisture through geophysics measurements. As roots of adult and younger trees reach different soil layers and different processes affect their growth (Callaway 1997; Sankaran et al. 2004), we may find differences in spatial distributions between size classes of trees. We focused on *Acacia sieberiana* that encroaches grasslands of KwaZulu-Natal in South Africa. The main question that we aimed to answer is: Does the spatial pattern of acacias depend on soil properties and soil moisture at different depths, and does this pattern change with acacia size?

2. Materials and methods

We studied the spatial relationships between acacias, soil properties and soil moisture over an area of 1.5 ha where electrical conductivity (EC) had previously been measured (*cf.* part II of this chapter). We obtained maps of EC representing soil properties, consisting mainly of clay content at 0-0.5 m (A horizon), 0.5-1.5 m and 0.8-1.5 m (B horizon) and 1-4 m depth (mainly colluvial bed rocks), and maps representing relative seasonal soil moisture for the same depth. All maps were extrapolated to obtain grids of the same spacing of 10 m using Surfer version 9 software (Golden Software 1993-2011).

All acacias were mapped using a differential global positioning system (DGPS) giving a high accuracy of the position (5 cm) in all three coordinates X, Y, Z. Regular grids of 10*50 m were delimited to map all acacias. Acacias were separated into different size classes according to the following criteria: the height of “tall” acacias was >3 m (this size class corresponds to more fecund acacias). The height of “medium” acacias was ranged between 1 and 3 m (they produce fewer pods than tall acacias and they are seldom eaten by cattle and goats). The height of “small” acacias was between 0.2 and 1 m (they do not produce any pod but cattle and goats have an easy access to their leaves). Acacia seedlings were < 0.2 m high (they can either be eaten or trampled by cattle and goats).

Once mapped, acacias of each size class were counted in an area of 5 m surrounding each value of conductivity using ArcGis 9.3 (ESRI 2008). It was thus possible to create a density map of acacias for each size and to link this density to soil properties. From the results we obtained, especially for medium-sized acacias, we found that there was an important influence of maximum density. Thus, we calculated the maximum acacia density for conductivity values with a step of 1 mS m^{-1}. Correlations between maximum acacia density and conductivity were tested with general additive models (GAM) using R software version 2.11 (R Development Core Team 2010, http://www.R-project.org).

Topography maps were obtained using regular spaced DGPS points from the area and kriging interpolation in Surfer 9 (Golden Software 1993-2011). To visually enhance the minor variations in mean topography, we adjusted using least-square regressions and removed the parabolic surface from the data.

3. Results

3.1 Acacia density map

The three size classes of acacias showed different patterns (Fig. 1). Tall acacias were mostly located in the south-eastern part and in the north-western part of the plot. Two areas (in white on Fig. 1a) had no tall acacias. Medium acacias mainly occurred at a high density in the north-western and central parts (Fig. 1b). Two areas had lower medium-sized acacia density (Fig. 1b). Small acacias followed the pattern of medium acacias, with a higher density in the central part of the plot (Fig. 1c). Seedlings were almost regularly dispersed on the plot with higher density in the north-eastern part of the plot (Fig. 1d).

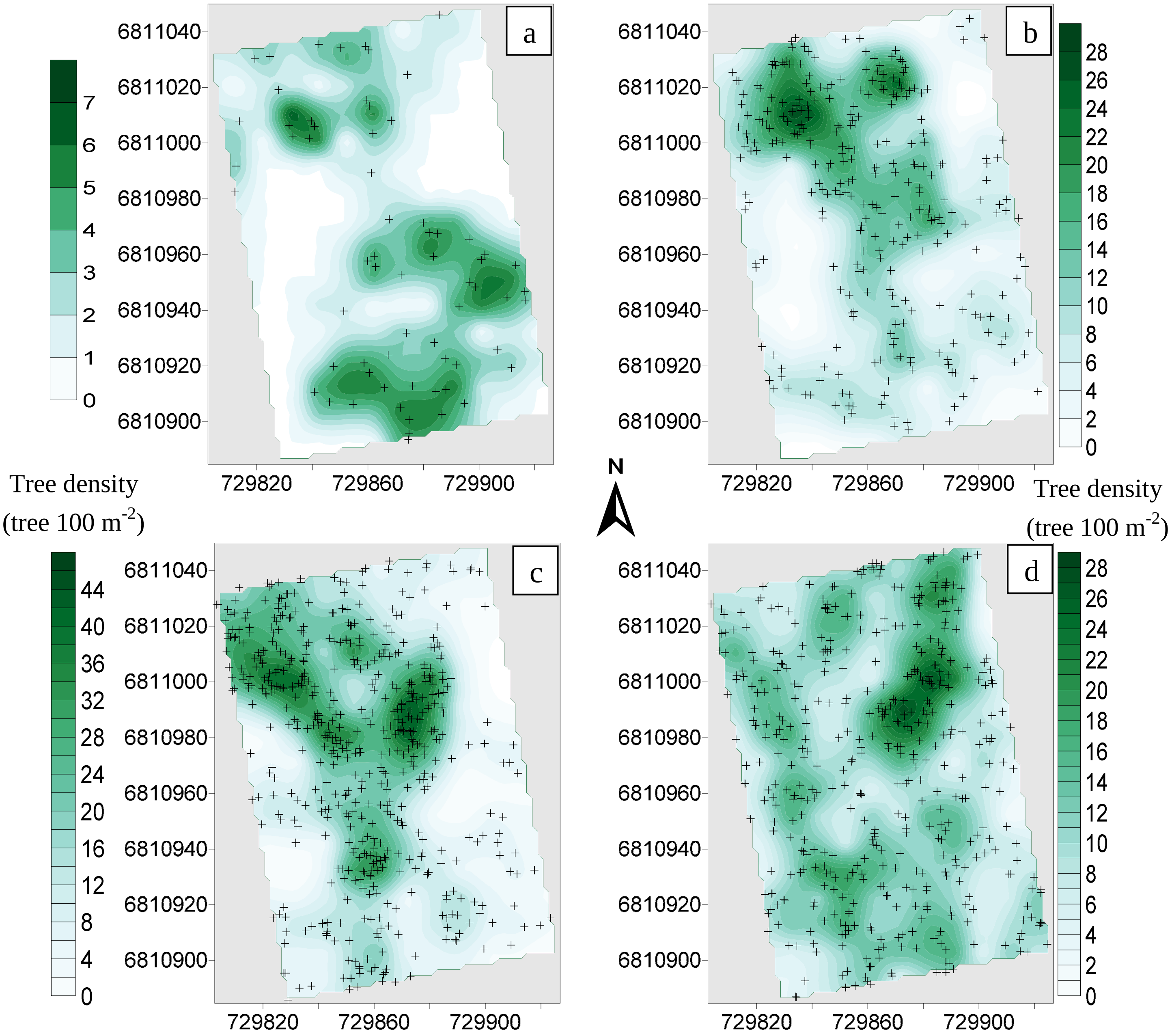
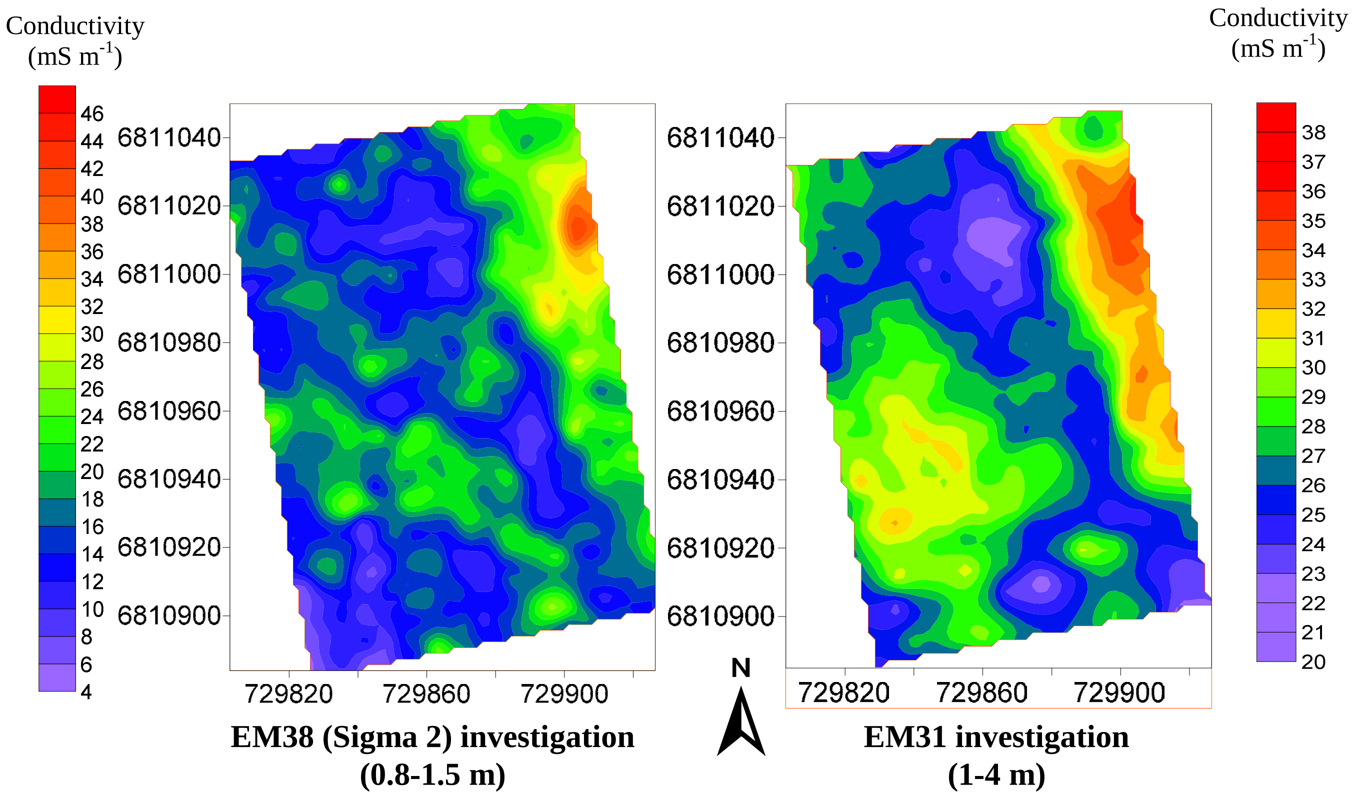


Figure 1. Acacia density map of the 1.5 ha area. a) Tall acacias > 3 m height. b) Medium acacias between 1 and 3 m height. c) Small acacias between 0.2 and 1 m height. d) Acacia seedlings < 0.2 m height. Crosses represent each acacia.

3.2 Correlations between acacia density and soil properties (clay content)

The results for conductivity and differences in conductivity for each soil layer were presented in the previous part of this chapter. As the conductivity of the first layer (0-0.5 m) (σ1) obtained during the dry season was very homogeneous, we did not correlate σ1 with tree density. The homogeneity of this first layer (which corresponds to the A horizon) indicates that this horizon did not show any clear heterogeneity in terms of soil properties related to conductivity. This is confirmed by the results of texture analysis from the three pits dug in the field (Appendix 1). Clay content, which most strongly influences the conductivity values during the dry season for non-saline soils (Corwin and Lesch 2005), was similar for the three pits in the uppermost 40-50 cm soil depths. Below 50 cm depth, conductivity or clay content had a higher spatial variability. σ2 at 0.5-1.5 m had similar patterns than σ2 at 0.8-1.5 m but with globally lower and less extreme values. Correlations with acacia density were very similar for both layers being higher with σ2 from 0.8-1.5 m. For that reason, we only present here the correlations with σ2 from 0.8-1.5 m depth. We displayed the two selected maps of conductivity for this study (Fig. 2).



EM38 (Sigma 2) investigation (0.8-1.5 m)

EM31 investigation (1-4 m)

Figure 2. Conductivity maps at 0.8-1.5 m and 1-4 m depths obtained with EM38-MK2 and EM31 respectively on a plot of 1.5 ha in the dry season. X and Y axes are the coordinates in UTM 35J.

The density of tall acacias plotted against the conductivity of the 0.8-1.5 m depth (Fig. 3a) showed that > 24.3 mS m^{-1} the density of tall acacias dropped to zero. The mean value of conductivity where tall acacias were present was 15.72 ±3.69 mS m^{-1}. A similar threshold was also observed at 1-4 m depth with a value at 31.9 mS m^{-1} (Fig. 3b) and a mean value of 26.88 ±2.09 mS m^{-1}. The conductivity values above these thresholds were found in the north-eastern part of the plot where conductivity reflects higher clay amount at both depths. Medium acacias did not show as clear a threshold but showed a decrease of the maximal density with an increase of conductivity (Fig. 3c and 3d).

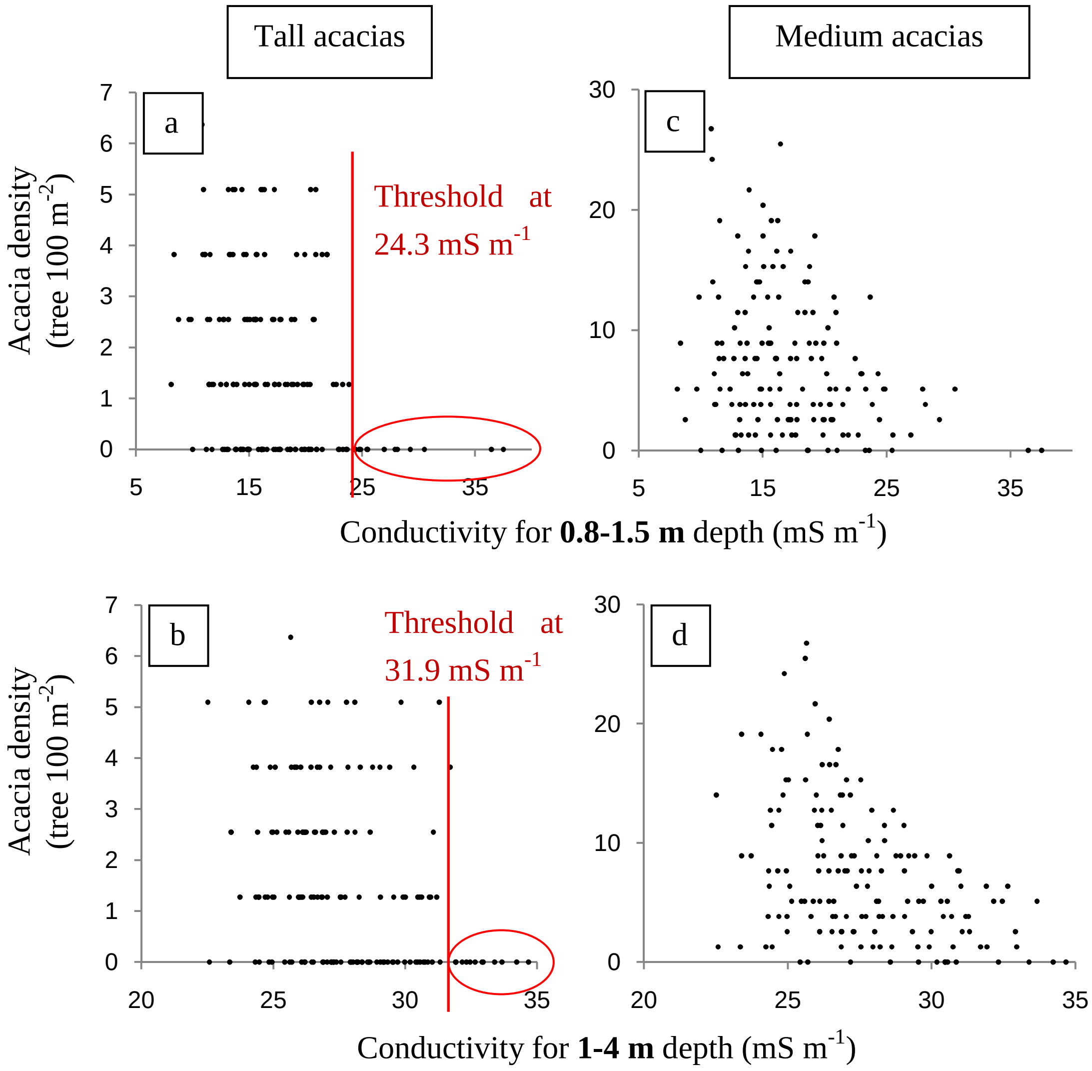


Figure 3. Tall and medium acacia densities (tree.100m^{-2}) are plotted against soil electrical conductivities (mS m^{-1}) for two depths: 0.8-1.5 m and 1-4 m. (a) Tall acacias at 0.8-1.5 m depths. (b) Tall acacias at 1-4 m depths. (c) Medium acacias at 0.8-1.5 m depths. (d) Medium acacias at 1-4 m depths.

We thus modeled the maximal densities of medium acacias with GAM (Fig. 4a and 4b). For the 0.8-1.5 m depths, the model was highly significant (F=18.74, p<0.0001) and explained 82.7 % of the deviance in maximum medium acacia density (Fig. 4a), being maximal at 14 mS m^{-1}. At 1-4 m depths (Fig. 4b), the model was highly significant (F=245.8, p<0.0001) and it explained 99.8 % of the deviance in maximum medium acacia density, with a miximum at 25 mS m^{-1}.

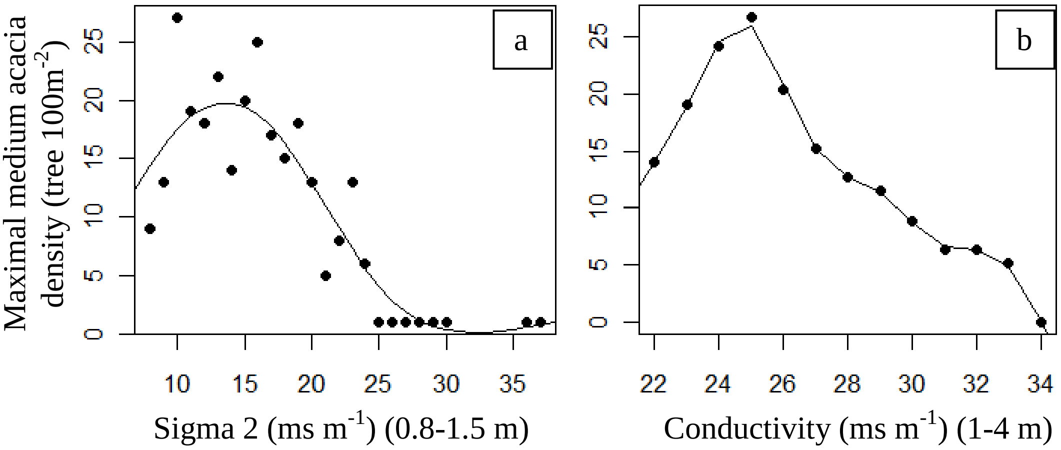


Figure 4. Maximum values of medium acacia density versus soil electrical conductivity. The best fit curve was estimated by GAM.

Small acacias showed a less clear pattern than taller acacias but similar thresholds to those of tall acacias were still visible (Fig. 5a and 5b). At 0.8-1.5 m depths, small acacia densities dropped below 10 trees 100 m^{-2} for conductivity values above 25 mS m^{-1}. For 1-4 m depths, the threshold was at 32 mS m^{-1}. Seedlings did not show any specific patterns (Fig. 5c and 5d).

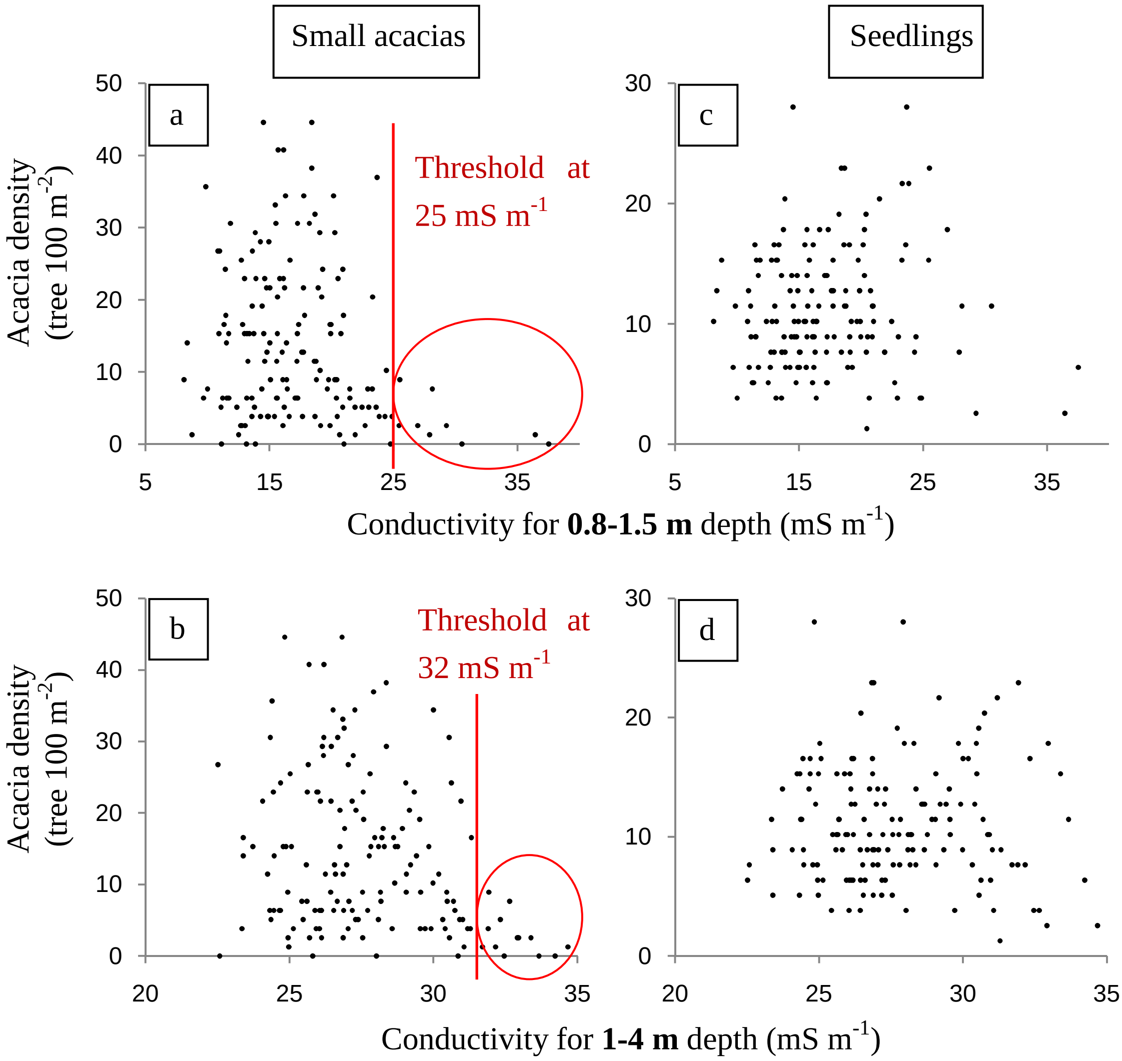
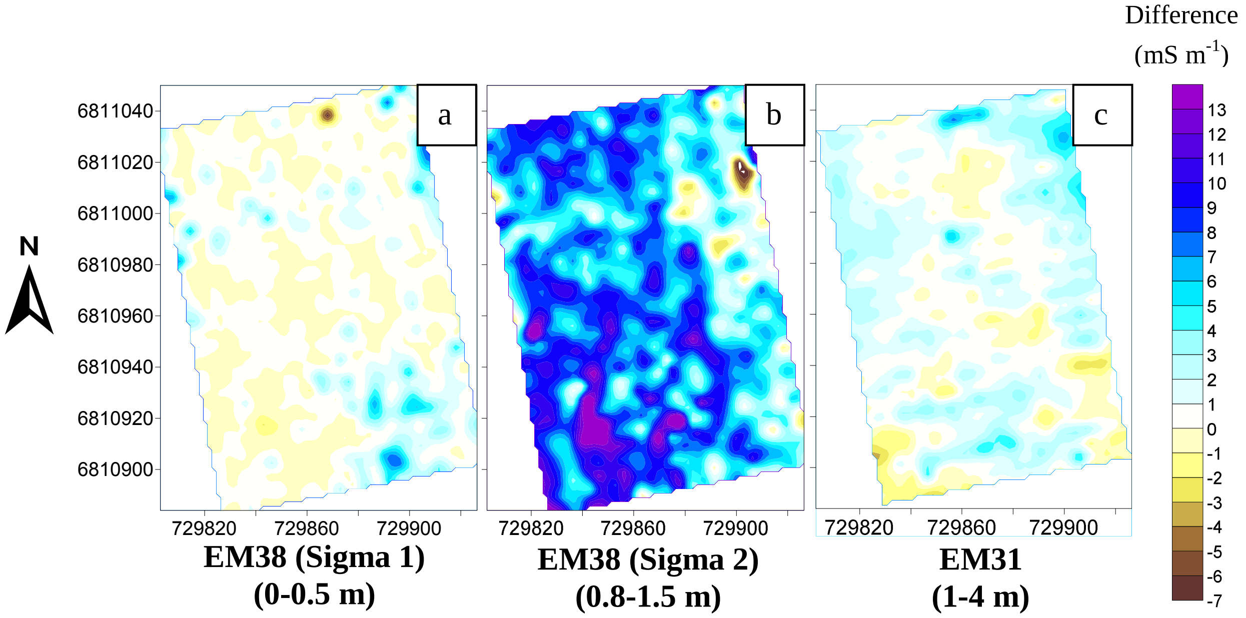


Figure 5. Small and seedlings acacia densities (tree.100m^{-2}) are plotted against the soil electrical conductivities (mS m^{-1}) for two depths: 0.8-1.5 m and 1-4 m. (a) Small acacias at 0.8-1.5 m depths. (b) Small acacias at 1-4 m depths. (c) Seedlings at 0.8-1.5 m depths. (d) Seedlings at 1-4 m depths.

3.3 Correlations between acacia density and relative seasonal soil moisture

As explained in part II of this chapter, seasonal soil moisture was higher at 0.8-1.5 m depths than at the surface and deeper than 1.5 m (Fig. 6). Tall acacias had a threshold only for 0.8-1.5 m depths which was at zero (Fig. 7b). For all negative values matching to higher seasonal soil moisture in the dry season, tall acacia density was zero. Medium acacias were slightly influenced by the first layer at 0-0.5 m depths (Fig. 7d), showing lower density values for greater differences in conductivity (above 3 mS m^{-1}), where seasonal soil moisture was the highest. Small trees and seedlings were both positively correlated with soil moisture of the uppermost layer (Fig. 8a and 8d) with decreasing density values with increasing seasonal soil moisture. The soil moisture of the deeper layer at 1-4 m did not affect any of the size classes of acacia.



EM38 (Sigma 1)
(0-0.5 m)

EM38 (Sigma 2)
(0.8-1.5 m)

EM31
(1-4 m)

Figure 6. Difference in soil electrical conductivities between the wet and the dry seasons for three depths of investigation: (a) 0-0.5 m, (b) 0.8-1.5 m and (c) 1-4 m depths obtained with EM38 and EM31 geophysical methods on a plot of 1.5 ha. X and Y axes are the coordinates in UTM 35J.

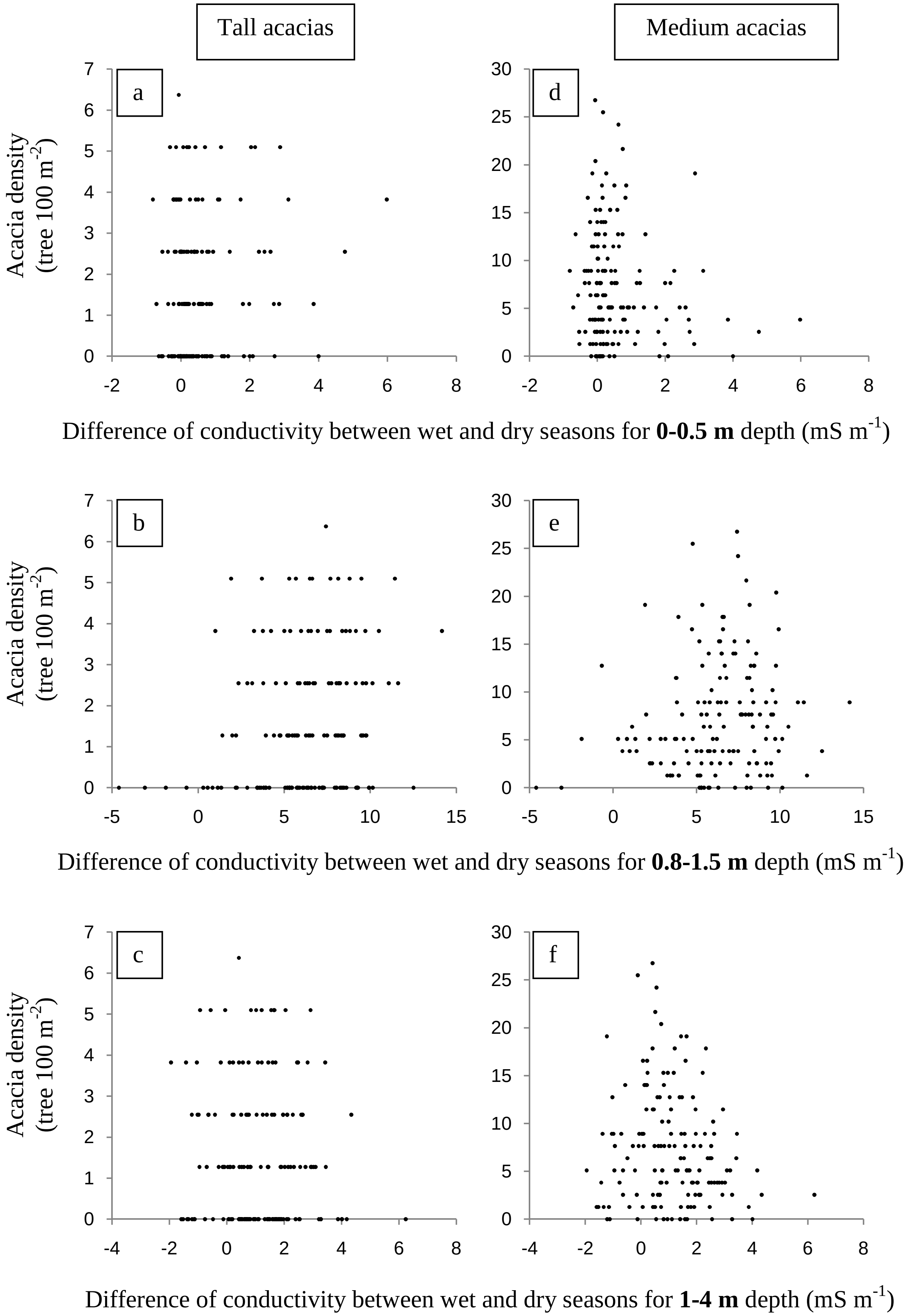


Figure 7. Tall and medium acacia densities (tree 100 m^{-2}) are plotted against the difference of soil electrical conductivities (mS m^{-1}) between the wet and the dry seasons for two depths: 0.8-1.5 m and 1-4 m.

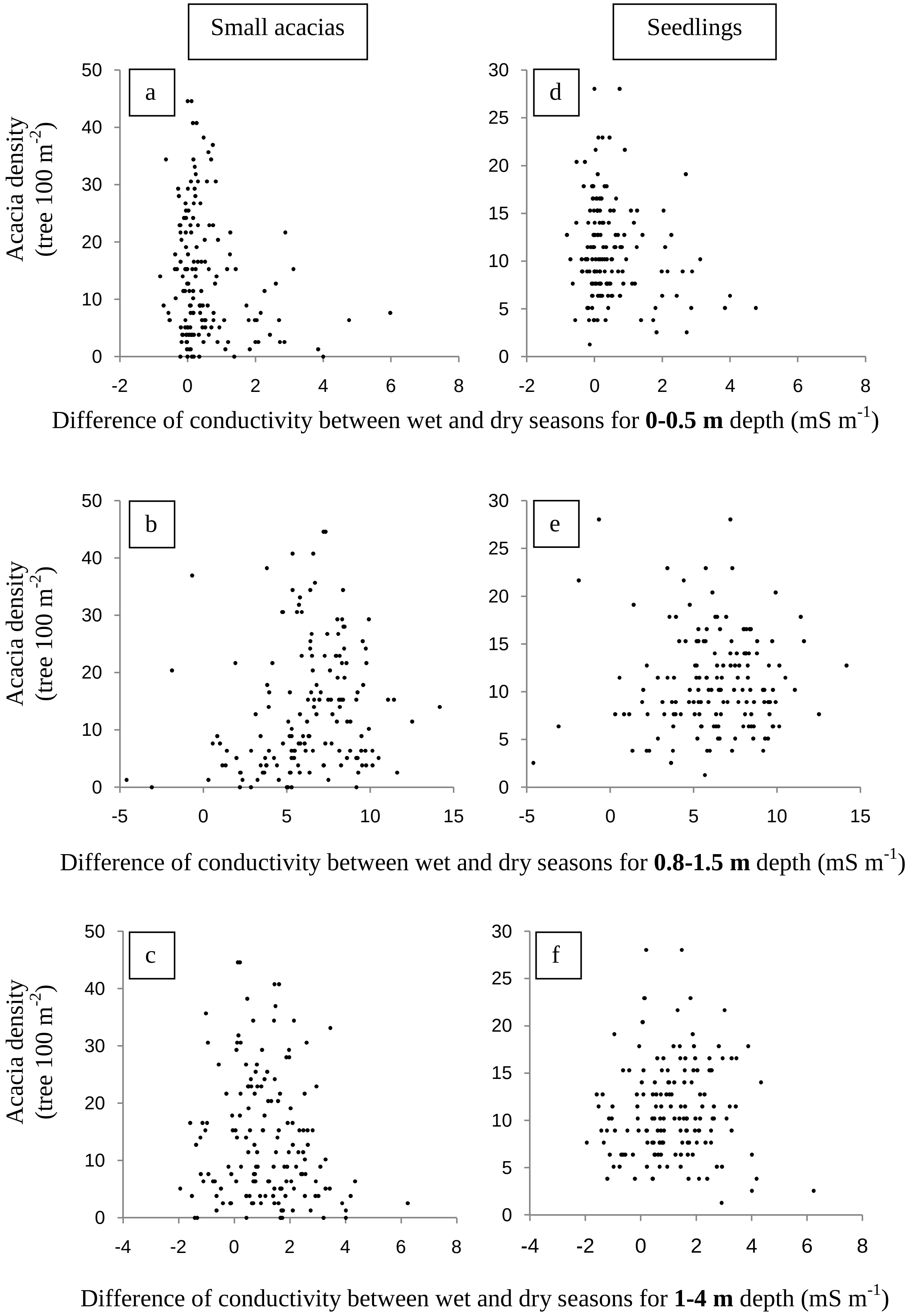


Figure 8. Small and seedling acacia densities (tree 100 m^{-2}) are plotted against the difference of soil electrical conductivities (mS m^{-1}) between the wet and the dry seasons for two depths: 0.8-1.5 m and 1-4 m.

4. Discussion

The different spatial patterns of trees in this study showed that seedlings and small acacias are located away from taller acacias. This suggests that competition under tall acacias may be too strong for small acacias to germinate and or survive (for similar results see e.g. Riginos et al., 2005).

The correlations between acacia densities and conductivities are consistent with the study of Robinson et al. (2010) regarding oaks growing in semi-arid areas near Stanford (California, USA). They showed that oaks in this savanna developed preferentially on soils with lower conductivity in the first 1 m (~21 mS m^{-1}) associated with lower clay content than areas where only grass was present (~32 mS m^{-1}). In our study, taller acacias with their deeper roots were most affected, with a net threshold of conductivity that limited their development (see e.g. Fig. 3a and 3b). Due to the increasing clay content with depth, the main limitation for tall acacia growth appears to be the higher values of conductivity at 1-4 m where the mean values where acacias are present was 26.88 mS m^{-1} and the threshold was 31.9 mS m^{-1}. Conductivities depend on both soil characteristics and properties (McNeill 1992; Lesch and Corwin 2003) making the comparison of absolute values between two different sites difficult.

Overall, medium acacias followed the same pattern as tall acacias but were not completely absent from the area of high conductivity (unlike tall acacias). Presumably, with their shallower roots, small acacias and seedlings were less affected by the high clay content in layers at 0.8-4 m depth. Differential mortality of size classes of acacias explains this pattern (Barot et al. 1999). Clay amount had a negative impact on acacia development which is linked to soil texture. Several studies have identified soil type as influencing tree populations either at the seedling stage (Kambatuku et al. 2011), or for the population at large (Schleicher et al. 2011). Clayey soils have a fine soil texture which determines the porosity, the saturated hydraulic conductivity and available soil moisture for plants (Saxton et al. 1986; Fernández-Illescas et al. 2001; Fravolini et al. 2005). Fine-textured soils, in contrast to coarse-textured soils, have smaller pores and limit the drainage of water. This is especially true on duplex soils with an upper sandier layer and a second more clayey layer, sometimes promoting waterlogging at the surface of the less permeable second layer (Cox and McFarlane 1995). In very fine-texture soils, tree roots may not grow as deep as in coarse-textured soils (Xu and Li 2008; Macinnis-Ng et al. 2010), limiting tree growth. While clay can have positive effects on nutrients and water availability (Bechtold and Naiman 2006), high clay content can also limit the access to water for trees and thus limit their development (Xu and Li 2008). Grass and smaller trees do not face this problem as they mainly explore the uppermost layer which is more permeable, with larger pores and with more available water (Chittleborough 1992; Gregory et al. 1992). In this grassland, clay content of the second and third layer is heterogeneous due to heterogeneous deposition of colluviums, which affects the spatial distribution of acacias.

Soil hydraulic properties, linked to soil texture, play a major role in modifying spatial and temporal availability of water to plants (Fravolini et al. 2005; Wu and Archer 2005; Robinson et al. 2010). Medium, small and seedling acacias were less dense in areas where soil moisture of the uppermost layer was highest (Fig. 7d, 8a and 8d). The south-eastern area of the study plot (Fig. 6a) did not match deeper layers with high clay content where water could have accumulated which may be the case for the small areas in the north-eastern part of the plot. The south-eastern area was not located on a topographic depression which could have enhanced soil moisture (data not shown). This suggests that, rather than looking at the impact of soil moisture on the spatial pattern of acacia population, we should look at the impact of trees on soil moisture in this uppermost layer. The difference in soil moisture between the dry and the wet seasons is very low indicating that herbaceous layers as well as acacias (that use part of the uppermost subsurface water (Grellier et al. in prep)) dry out the first layer during the growing season. Other drainage and evaporation processes may also contribute to this result (Ward and Dunin 2001) during the wet and hot season which is the growing season in this habitat. For a reason that is not explained by the abiotic factors studied here, lower densities of medium, small and seedling acacias were found in this area, which is thus not completely dried out by reduced acacia transpiration.

The deeper soil moisture at 0.8-1.5 m depths mainly affected tall acacias is partially linked to clay content. The north-eastern part of the plot had higher soil moisture in the dry season (negative values on Fig. 6b) that we considered to be linked to the retention properties of such clayey soils in Part II of this chapter. Because of the high clay content, low porosity and thus low hydraulic properties of this kind of layer, tall acacias do not established at all.

5. Conclusions

In this mesic grassland, the distribution of taller acacias is mainly driven by the heterogeneity in clay content of soil layers at 1-4 m depth. Soil moisture, besides influencing the spatial pattern of the *A. sieberiana* population, was influenced by smaller acacias in the surface layer. Duplex soils induce specific soil properties that influence the spatial pattern of taller acacias that depend on deeper layers. We can thus answer the question we asked in the introduction: soil properties, especially clay content at different depths affect the spatial pattern of *A. sieberiana* differently according to their size.

These results could aid our understanding and prediction of the spatial distribution of acacias during encroachment. Focusing management practices on these areas particularly favorable to the taller acacias should be more effective. Finally, these results confirm that using geophysical tools in ecology allows for large scale investigations.

In order to investigate further the question and to extend the results to a larger scale, several improvements could be made. Developments of the inversion software are possible by taking three soil layers into account, for example. We could not have done this here but due to the particularity of the transition layer between the first and the second layer, it could have improved the interpretation.

6. References

Archer, S. 1995. Tree-grass dynamics in a Prosopis-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83-99.

Barot, S., J. Gignoux and J-C. Menaut. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. Ecology 80: 1987-2005.

Bechtold, J. S., Naiman, R. J. 2006. Soil texture and nitrogen mineralization potential across a riparian toposequence in a semi-arid savanna. Soil Biology and Biochemistry 38: 1325-1333.

Breshears, D. D., O. B. Myers and F. J. Barnes. 2009. Horizontal heterogeneity in the frequency of plant-available water with woodland intercanopy-canopy vegetation patch type rivals that occuring vertically by soil depth. Ecohydrology 2:503-519.

Briggs, J. M., H. Schaafsma and D. Trenkov. 2007. Woody vegetation expansion in a desert grassland: Prehistoric human impact? Journal of Arid Environments 69:458-472.

Britz, M.-L. and D. Ward. 2007. Dynamics of woody vegetation in a semi-arid savanna, with a focus on bush encroachment. African Journal of Range and Forage Science 24:131-140.

Brown, J. R. and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. Ecology 80:2385–2396.

Browning, D. M., S. R. Archer, G. P. Asner, M. P. McClaran and C. A. Wessman. 2008. Woody plants in grasslands: post-encroachment stand dynamics. Ecological Applications 18:928-944.

Callaway, R. M. and L. R. Walker. 1997. Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958-1965.

Chittleborough, D. J. 1992. Formation and pedology of duplex soils. Australian Journal of Experimental Agriculture 32:815-825.

Corwin, D. L. and S. M. Lesch. 2005. Apparent soil electrical conductivity measurements in agriculture. Computers and Electronics in Agriculture 46:11-43.

Cox, J. W. and D. J. McFarlane. 1995. The causes of waterlogging in shallow soils and their drainage in southwestern Australia. Journal of Hydrology 167:175-194.

Eggemeyer, K. D. and S. Schwinning. 2009. Biogeography of woody encroachment: why is mesquite excluded from shallow soils? Ecohydrology 2:81-87.

ESRI. 2008. ArcMap-ArcEditor, Environmental Systems Research Institute, Inc. New York, USA.

Fernández-Illescas, C. P., A. Porporato, F. Laio and I. Rodríguez-Iturbe. 2001. The ecohydrological role of soil texture in a water-limited ecosystem. Water Resource Research 37:2863-2872.

Fravolini, A., K. R. Hultine, E. Brugnoli, R. Gazal, N. B. English and D. G. Williams. 2005. Precipitation pulse use by an invasive woody legume: The role of soil texture and pulse size. Oecologia 144:618-627.

Gignoux, J., G. Lahoreau, R. Julliard and S. Barot. 2009. Establishment and early persistence of tree seedlings in an annually burned savanna. Journal of Ecology 97:484-495.

Golden Software Inc, 1993-2011. Surfer Version 9. 809 14th Street Golden, CO 80401-1866 USA.

Graz, F. P. 2008. The woody weed encroachment puzzle: gathering pieces. Ecohydrology 1:340-348.

Gregory, P. J., D. Tennant, A. P. Hamplin and J. Eastham. 1992. Components of the water-balance on duplex soils in western Australia. Australian Journal of Experimental Agriculture 32:845-855.

Grellier, S., J. L. Janeau, P. Richard, D. Ward, T. Bariac and S. Lorentz. Water uptake adaptations of *Acacia sieberiana* in a woody plant encroached grassland of South Africa. Ecohydrology: in prep.

Grellier, S., J. L. Janeau, S. Barot and D. Ward. Grass competition is more important than animal dispersal. Oecologia: submitted.

Halpern, C. B., J. A. Antos, J. M. Rice, R. D. Haugo and N. L. Lang. 2010. Tree invasion of a montane meadow complex: temporal trends, spatial patterns, and biotic interactions. Journal of Vegetation Science 21:717-732.

Higgins, S. I., W. J. Bond and W. S. W. Trollope. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88:213-229.

Jeltsch, F., S. J. Milton, W. R. J. Dean and N. Van Rooyen. 1996. Tree spacing and coexistence in semiarid savannas. Journal of Ecology 84:583-595.

Kambatuku, J. R., M. D. Cramer and D. Ward. 2011. Savanna tree–grass competition is modified by substrate type and herbivory. Journal of Vegetation Science 22:225-237.

Kraaij, T. and S. J. Milton. 2006. Vegetation changes (1995-2004) in semi-arid Karoo shrubland, South Africa: Effects of rainfall, wild herbivores and change in land use. Journal of Arid Environments 64:174-192.

Lesch, S. M. and D. L. Corwin. 2003. Using the dual-pathway parallel conductance model to determine how different soil properties influence conductivity survey data. Agronomy Journal, 95: 365-379.

Lin, H. 2006. Temporal stability of soil moisture spatial pattern and subsurface preferential flow pathways in the shale hills catchment. Vadoze Zone Journal 5:317-340.

Ludwig, F., T. E. Dawson, de Kroon H., F. Berendse and H. H. T. Prins. 2003. Hydraulic lift in *Acacia tortilis* trees on an East African savanna. Oecologia 134:293–300.

Macinnis-Ng, C. M. O., S. Fuentes, A. P. O'Grady, A. R. Palmer, D. Taylor, R. J. Whitley, I. Yunusa, M. J. B. Zeppel and D. Eamus. 2010. Root biomass distribution and soil properties of an open woodland on a duplex soil. Plant and Soil 327:377-388.

McNeill, J. D. 1992. Rapid, accurate mapping of soil salinity by electromagnetic ground conductivity meters. In: advances in measurement of soil physical properties: bringing theory into practice, specific publication 30, Soil Science Society of America, Madison, Wisconsin: 209-229.

Meyer, K. M., K. Wiegand, D. Ward and A. Moustakas. 2007. SATCHMO: a spatial simulation model of growth, competition, and mortality in cycling savanna patches. Ecological Modelling 209:377-391.

Nadezhdina, N., T. S. David, J. S. David, M. I. Ferreira, M. Dohnal, M. Tesar, K. Gartner, E. Leitgeb, V. Nadezhdin, J. Cermak, M. S. Jimenez and S. D. Morale. 2010. Trees never rest: the multiple facets of hydraulic redistribution. Ecohydrology 3:431-444.

Riginos, C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. Ecology 90:335–340.

Riginos, C., S. J. Milton and T. Wiegand. 2005. Context-dependent interactions between adult shrubs and seedlings in a semi-arid shrubland. Journal of Vegetation Science 16:331-340.

Riginos, C., S. J. Milton and T. Wiegand. 2005. Context-dependent interactions between adult shrubs and seedlings in a semi-arid shrubland. Journal of Vegetation Science 16:331-340.

Robinson, D. A., C. S. Campbell, J. W. Hopmans, B. K. Hornbuckle, S. B. Jones, R. Knight, F. Ogden, J. Selker and O. Wendroth. 2007. Soil moisture measurement for ecological and hydrological watershed-scale observatories: a review. Vadose Zone Journal 7:358-389.

Robinson, D. A., H. Abdu, S. B. Jones, M. Seyfried, I. Lebron and R. Knight. 2008. Eco-geophysical imaging of watershed-scale soil patterns links with plant community spatial patterns. Vadose Zone Journal 7:1132-1138.

Robinson, D. A., I. Lebron and J. I. Querejeta. 2010. Determining soil–tree–grass relationships in a California oak savanna using eco-geophysics. Vadose Zone Journal 9:1-8.

Sankaran, M., J. Ratnam and N. P. Hanan. 2004. Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7:480-490.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higging, X. L. Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea,

J. Tews, J. Worden and N. Zambatis. 2005. Determinants of woody cover in African savannas. Nature 438:846-849.

Saxton, K. E., W. J. Rawls, J. S. Romberger and R. I. Papendick. 1986. Estimating generalized soil water characteristics from texture. Soil Science Society of America Journal 50:1031-1036.

Schleicher, J., K. Wiegand and D. Ward. 2011. Changes of woody plant interaction and spatial distribution between rocky and sandy soil areas in a semi-arid savanna, South Africa. Journal of Arid Environments 75:270-278.

Snyman, H. A. 2009. Root studies on grass species in semi-arid South Africa along a soil-water gradient. Agriculture, Ecosystems and Environment 131: 247-254.

Trinogga, J. 2010. Arid savanna shrubs affect soil chemistry and vegetation cover. School of Biology and Pharmacy, Master thesis. Friedrich Schiller University, Jena, Germany.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931-2942.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, UK.

Ward, D. 2005. Do we understand the causes of bush encroachment in African savannas? African Journal of Range and Forage Science 22:101-105.

Ward, P. R. and F. X. Dunin. 2001. Growing season evapotranspiration from duplex soils in south-western Australia. Agricultural Water Management 50:141-159.

Wiegand, K., D. Saltz and D. Ward. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7:229-242.

Wiegand, K., D. Ward and D. Saltz. 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. Journal of Vegetation Science 16:311-320.

Wu, X. B. and S. R. Archer. 2005. Scale-dependent influence of topography-based hydrologic features on patterns of woody plant encroachment in savanna landscapes. Landscape Ecology 20:733–742.

Xu, G. Q. and Y. Li. 2008. Rooting depth and leaf hydraulic conductance in the xeric tree *Haloxyolon ammodendron* growing at sites of contrasting soil texture. Functional Plant Biology 35:1234-1242.

Young, M. H., D. A. Robinson and R. J. Ryel. 2010. Introduction to coupling soil science and hydrology with ecology: toward integrating landscape processes. Vadose Zone Journal 9:515-516.

Chapitre 4. Les facteurs de contrôle de l'invasion ligneuse

Jeune plantule d'*Acacia sieberiana* possédant encore ses deux cotylédons.

Le chapitre précédent a permis d'établir un état des lieux de l'écosystème étudié à une large échelle spatiale et temporelle montrant à la fois l'évolution des ravines et de la population d'*A. sieberiana* et le rôle des propriétés du sol sur la répartition des acacias. Afin de comprendre plus finement certains mécanismes intervenant sur le système « arbre-herbe », nous allons aborder dans le présent chapitre, l'inter-compétition (compétition arbre-herbe) qui pourra être déterminante pour l'évolution de l'invasion ligneuse. L'approche multi-facteurs est le meilleur moyen de mettre en évidence des interactions entre les principaux facteurs de contrôle de l'invasion ainsi que leur importance respective dans cet écosystème semi-humide. La première partie présente une étude multi-facteurs comprenant le feu, l'herbivorie (simulant à la fois la réduction du couvert herbacé et le transit intestinal des graines) et les nutriments (par apport de bouses de vache) en testant leurs différents effets et interactions sur des stades déterminants de la population d'*A. sieberiana,* c'est-à-dire la germination et la croissance de jeunes plantules. Toujours dans un but de compréhension des facteurs de contrôle de la population d'*A. sieberiana*, la deuxième partie traite de l'étude du facteur « eau » et plus précisément de la ressource en eau du sol. Cette étude écohydrologique cherche à montrer comment les arbres utilisent la ressource en eau (profondeur de prélèvement de l'eau) en fonction de leur taille et de leur position dans le bassin versant afin de mettre en évidence de possibles adaptations favorisant l'invasion ligneuse. Il s'agit donc de deux démarches différentes mais qui permettront des avancées scientifiques dans la compréhension des facteurs de contrôle de l'invasion ligneuse.

I. L’étude des principaux facteurs influençant le stade jeune plantule

Grass competition is more important than animal dispersal

Séraphine Grellier[1], Sébastien Barot[2], Jean-Louis Janeau[1], David Ward[3]

[1]IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Scottsville, South Africa
[2]IRD-BIOEMCO, Ecole Normale Supérieure, Paris, France
[3]School of Biological & Conservation Sciences, University of KwaZulu-Natal, Scottsville, South Africa

Keywords: *Acacia sieberiana*; encroachment; fire; germination; grassland

Submitted in a reduced format to Oecologia and accepted with major corrections.

Abstract

Numerous models have suggested that fire and herbivory play an important role in tree encroachment in grasslands. However, little field data are available to support these assumptions. Furthermore, interactions between fire and herbivory are not well understood. We tested the effects of fire, grass, cattle ingestion (digestive transit) and dung (as a source of nutrients) on germination as well as growth and mortality of *Acacia sieberiana* seedlings in a subhumid grassland of South Africa. About 8000 seeds were planted in the field in a randomized block design. A similar experiment with cattle ingestion and dung treatments was undertaken in a shadehouse. Frequency of natural rainfall was an important factor influencing germination and seedling mortality in the first growing season. Fire and grass decreased seedling survival through burning, heat and competition for light, water and nutrients. In the shadehouse, cattle had a positive effect on germination through the combination of gut transit (which removes the hard seed coat) and dung (which supplies nutrients) and may thus promote tree encroachment. In the field, we found that transit through cattle did not have an important effect. Competition with grass had a far stronger negative effect on seedling survival. Although it is often claimed that gut passage through animals is a key factor of tree success in grassland and savannas, the removal of grass by grazing and/or fire had a far more important effect on acacia recruitment.

1. Introduction

Woody plant encroachment is widespread on most continents (Archer et al. 1995; Bond 2008). The impact of woody plants on grassland ecosystems is of great concern for human and wildlife as encroached areas are an important resource for domestic livestock and wild herbivores (Van Auken 2009). Trees decrease the available grazing area (Kraaij and Ward 2006; Wigley et al. 2009) having economical consequences on ranch yield (Burkinshaw and Bork 2009). While some authors describe trees as “islands of fertility” due to their positive effects on nutrient availability (Treydte et al. 2007; Ravi et al. 2010), others have reported negative consequences for the precarious balance of ecosystem functioning (Scholes and Archer 1997; Smit 2004). Effects are highly variable and depend on climate, location, tree density and site specificity (Smit 2004). Managers try to mitigate the negative impacts of tree encroachment by tree eradication (Smit 2004) or attempt to take advantage of the positive impact of trees on nutrient availability by maintaining trees at a specific density (Treydte et al. 2007). However, management can only be conducted efficiently if the causes of woody plant encroachment are well understood. There is consensus that water, nutrients, fire and herbivory are key variables of tree-grass balance in grasslands (Sankaran et al. 2004; Ward 2005; Wiegand et al. 2006). Other factors have also been recorded to influence tree populations, such as rodents (Goheen 2004) or bruchid beetles (Coe and Coe 1987; Or and Ward 2007) that feed on *Acacia* seeds and destroy them.

There is thus little consensus on the four main factors cited above and their relative influence. Different models have been proposed to explain the coexistence of trees and grasses and changes in tree densities: (1) Competition models such as the two layer model of Walter (1971) are based on rooting niche separation but cannot be generalized (Sankaran et al. 2004; Ward 2005), especially in wetter areas where water availability reduces competition between grass and trees (Jeltsch et al. 1996) and in areas where the soil is too shallow to allow separation of tree and grass roots (Wiegand et al. 2005). (2) Demographic-bottleneck models are based on different impacts of climatic variability and disturbances between life-history stages of trees which are essential in the tree-grass equilibrium (Higgins et al. 2000; Sankaran et al. 2004; Gignoux et al. 2009). (3) Other models consider grasslands or savannas as patch-dynamic systems (Wiegand et al. 2006; Meyer et al. 2007) where landscapes are composed of many patches in different transition states between grassy and woody dominance.

Sankaran et al. (2005) suggested a global model for African savannas where mean annual precipitation (MAP) is the main determinant of woody plant encroachment: trees in dry areas (MAP<650mm) are limited to a maximal density by MAP, whereas trees in mesic areas (MAP>650mm) are not limited by water and will be driven by disturbances such as fires and herbivores. In such “disequilibrium” systems, inter-annual climatic variability, fire and herbivory limit germination, seedling survival and sapling growth and, thus, the transition to mature trees (Sankaran et al. 2004; Prior et al. 2009). However, the respective influence of these disturbances and their interactions are not well understood due to the scarcity of field data and the complexity of the interactions.

Multi-factorial experiments, taking fire and herbivores into account, have been emphasized as the only way to study the causes of woody encroachment (Ward 2005; Kraaij and Ward 2006) especially on seed and seedling stages which are a prerequisite for an increase in tree abundance and are very influential in the process of woody encroachment (Kraaij and Ward 2006). Herbivores are often studied for their grazing activities (Mbatha and Ward 2010) that drive competition between grass and trees (Kraaij and Ward 2006; Riginos 2009; Goheen et al. 2010). However, herbivores can also affect tree dynamics through their effects on seeds: seed transit via large mammals and seed deposition in dung may indeed enhance seed germination and survival and subsequent recruitment (Halevy 1974; Miller and Coe 1993; Andresen 2001; Or and Ward 2003; Bodmer and Ward 2006). To better understand and clarify the mechanisms involved, we studied the encroaching *Acacia sieberiana* seedling establishment, a tree that is common in subhumid grasslands in KwaZulu-Natal (South Africa). Our study manipulates passage through animals (hereafter called *Transit*), presence or absence of animal faeces (*Dung*), competition with grasses (Grass), *Fire* and tests their effects on seed germination, seedling growth and mortality.

2. Materials and methods

2.1 Study site

The study site is located in a commercial grassland 8 km south-east of Bergville (28º 47' 14" S; 29º 22' 38" E) and is included in the Tugela basin (30,000 km²). The altitude of the site is 1235 m and is representative of the grassland biome present in the KwaZulu-Natal Drakensberg foothills. The vegetation of the site belongs more specifically to the Northern KwaZulu-Natal moist grassland (Mucina and Rutherford 2006). The climate is subhumid subtropical with four seasons and a rainy summer (October–April). The mean annual precipitation calculated for the last 65 years is 745 mm. The mean annual temperature is 13 °C (Schulze et al. 1997). Potential evaporation is between 1600 mm and 2000 mm (Guy and Smith 1995). Encroachment by *Acacia sieberiana* var. *woodii* (Burtt Davy) Keay & Brenan is observed in the valley, especially in the adjacent communal grassland. The main grass species on the site were *Hyparrhenia hirta* (L.) Stapf, *Cymbopogon excavatus* (Hochst.) Stapf ex Burtt Davy, *Eragrotis curvula* (Schrad.) Nees, *Eragrotis plana* Nees and *Sporobolus africanus* (Poir.) Robyns & Tournay. The general soil type is a luvisol (World Reference Base 1998) with two well-delimited main horizons. This grassland is exclusively grazed by cattle.

2.2 Experimental design in the field

Two identical large fenced plots 20 m by 20 m were installed in the grassland, one on an area burnt every year for at least 12 years (burnt plot) and the other on an area not burnt for at least 5 years (unburnt plot). These plots were 20 m apart. This constitutes our first treatment (1) *Fire* vs. *No-Fire*. Within each large plot, three other treatments were studied according to a completely-crossed randomized block design with three replicates per treatment: (2) *Grass* vs. *No-Grass*; (3) *Dung* vs. *No-Dung*; (4) *Transit* seeds vs. *No-Transit*. The three other treatments applied in this study were as follows:

Grass vs. *No-Grass*

Absence of grass simulates an indirect effect of grazing. Twenty four plots were cut manually before planting and then every month to keep the grass as short as possible during the experiment. Attention was made to conserve all seedlings and cut the grass around them.

Dung vs. *No-Dung*

Dung collected from the Ukulinga research farm of the University of KwaZulu-Natal in Pietermaritzburg were used to ensure the absence of *A. sieberiana* in the dung as the study area was not previously encroached. We applied 60 cm^3 of fresh dung on each seed in 24 plots just after planting to simulate the effect of dung on a seed just after transit.

Transit vs. *No-Transit*

Transit seeds were collected in the adjacent grassland encroached by *A. sieberiana* in an area where cattle rest and deposit dung. Molar teeth marks observed on seeds confirmed that all seeds were ingested by cattle. *No-Transit* seeds were collected in the same grassland directly from pods that were lying on the ground under trees (to ensure maturity of seeds). Pods were opened and seeds were removed. All *Transit* and *No-Transit* seeds were sorted in the laboratory to exclude seeds that were either infested by bruchid beetles, germinated or mechanically damaged. As both types of seeds were harvested in June 2009, once sorted, they were kept in the refrigerator until planting in October 2009. Viability tests of sub-samples (150 *Transit* seeds and 150 *No-Transit* seeds) were conducted in the laboratory. After clipping of one extremity, seeds were cultivated in petri dishes on agar gel at 25 °C for 10 days.

Taken together, this experimental design comprised 48 plots (24 burnt, 24 not burnt with three replicates of each treatment combination). Each of the 48 plots was 1 m by 2 m in size. All plots were separated from each other by a 1 m-wide buffer zone. Seeds were planted 10 cm apart in parallel lines at 1 cm depth in the soil and covered by soil (or dung if it was a *Dung* treatment plot). One hundred and sixty seeds were planted per plot, making a total of 7680 seeds.

2.3 Monitoring of field experiment

The field experiment lasted for one year. All seeds were monitored every week at the beginning of the experiment and then every month to record germinated seeds, seedling heights, and mortality until June 2010. An extra record was achieved in November 2010 at the beginning of the wet season to assess seed germination and seedling growth after the dry season and one burning event in burnt plots.

Due to potential soil surface differences between burnt plots and unburnt plots, we described soil surface features of the 48 plots. Expert judgment visually estimated in February 2010 the percentage cover of the main features including soil crust, vegetation cover, micro-aggregates and undecomposed dung (usually dry dung), based on the classification of Valentin and Bresson (1992).

2.4 Shadehouse experiment

We set up an experiment in the more controlled environment of a shadehouse for two years to test for the effect of dung and transit on seed germination. We tested the *Dung* factor (as discussed for the field experiment) and a *Seed* factor with three treatments on *A. sieberiana* seed germination: *Transit* (seeds were ingested and had passed through the cow's rumen), *Acid* (seeds were soaked in 1 M sulphuric acid solution for 60 min to make the seed coat water-permeable (Brown 1965)), *Control* (no specific treatment was used). Two thousand seeds were planted, consisting of 700 *Acid* seeds, 450 *Transit* seeds and 850 *Control* seeds, (half of each treatment planted in dung). Seeds were collected in June 2008 (one year prior to the seeds being collected for the field experiment) on the same grassland encroached by *A. sieberiana*. *Control* and *Acid* seeds were harvested as described above for the field experiment. *Transit* seeds came from pods collected on the ground and given to cattle from Ukulinga research farm, University of KwaZulu-Natal, Pietermaritzburg, South Africa. Cattle weighed between 250-300 kg. Seeds were harvested from their dung five to eight days after ingestion. All seeds were separated in the laboratory to exclude bruchid-infested seeds and damaged seeds. Planting was done at the beginning of the wet season in 2008 in pots of 5 cm diameter (two seeds per pot) and filled with disturbed soil collected in the studied grassland from the first 10 cm and sieved at 4 mm to exclude all *A. sieberiana* seeds. Daily watering was conducted during the wet season (October to April) with complete cessation of watering during the dry season (May to September). Seeds were followed weekly during the wet season. The number of germinated seeds and dead seedlings were recorded for two years.

2.5 Statistical analyses

All statistical analyses were done with R version 2.12.1 (R Development Core Team 2010). The effect of the four treatments on the probability of seeds germination, seedlings mortality and seedlings survival (germination minus mortality) was analyzed at the end of the first growing season (June 2010) and after the dry season (November 2010) by Nested

ANOVA with a mixed effects model (binomial model for binary response variables) with a random term for plots nested within *Fire* (large plots).

Effects of the four treatments on maximal height reached by *A. sieberiana* seedlings in the field during the growing season and on height of seedlings after the dry season were analyzed by nested ANOVA (GLIM) with a random term for plots nested within *Fire* (large plots). However both variables had non-normal residuals and heterogeneity of variance. Consequently, height after the dry season was Box-Cox transformed (λ=0.44). No transformation worked on maximal heights so we used Kruskal-Wallis non-parametric tests for this variable. Due to the nesting of treatments within the *Fire* treatment, we first tested for the *Fire* effect with a non-parametric Kruskal-Wallis test and then tested the three other factors separately for each large plot (*Fire* and *No-Fire*) with further Kruskal-Wallis tests. For the same reason, Kruskal-Wallis non-parametric tests were applied to test for the effect of *Fire* on soil variables due to non-normal residuals and heterogeneity of variance even after appropriate transformations.

The effects of “*Dung*’’ and “*Seeds*” factors on the probability of germination in the shadehouse at the end of each year were tested by two-way ANOVA with a generalized linear binary model. A *post hoc* χ^2 test was used to test for each treatment of the factor *Seeds*.

3. Results

3.1 Field experiment

The viability test for *Transit* seeds of *A. sieberiana* was significantly higher than for *No-Transit* seeds, with 98.7% and 79% germination, respectively (X^2 =17.5, p=<0.001).

Percentage of structural crusts (*Fire*: 26.3 ±15.9 %, *No-fire*: 3.9 ±6.1 %) and percentage of vegetation cover (*Fire*: 67.6 ±11.9 %, *No-fire*: 92.6 ±7.4 %) were significantly different between *Fire* and *No-Fire*. The percentage of crusts was significantly higher in *Fire* plots (obs. dif.=19.91, critical dif. =7.92) while vegetation cover was lower in *Fire* plots (obs. dif.=22.5, critical dif.=7.92). Percentage of dung (*Fire*: 4.3 ±4.7 %, *No-fire*: 1.0 ±1.5 %) and of soil micro aggregates (*Fire*: 1.7 ±3.2 %, *No-fire*: 2.5 ±3.5 %) did not differ significantly.

3.1.1 Rainfall effects and seasonal changes in germination and mortality for 2009-2010

From the beginning of the experiment (15th October, week 1) to the survey in April (after 22 weeks), rainfall increased regularly except between the 14th and the 18th weeks, where the rainfall amount stayed almost constant. Thereafter, and until the end of the growing season, rainfall decreased drastically to be close to zero in June 2010 in this summer rainfall area of the Southern Hemisphere. Over the growing season, germination of all treatments showed a similar tendency, with an important decrease at week 18 in February (Fig. 1). This event was associated with a high peak of seedling mortality during the same period (Fig. 2). This mortality peak for a single census represented 56% of the dead seedlings for the whole growing season (10 censuses in total).

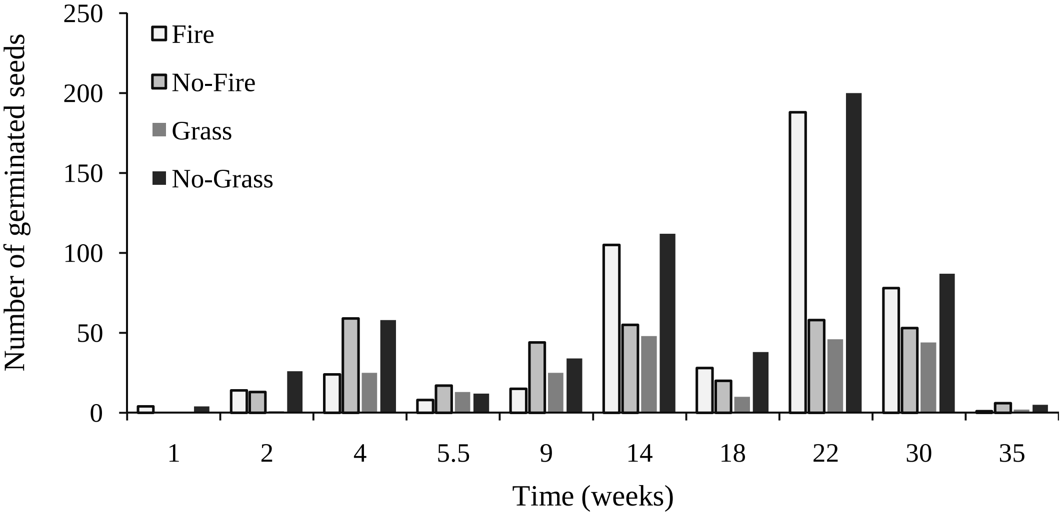


Figure 1. Change in the number of germinated *Acacia sieberiana* seeds over the growing season (from 15th October 2009 to 15th June 2010) for two treatments, *Fire* and *Grass*.

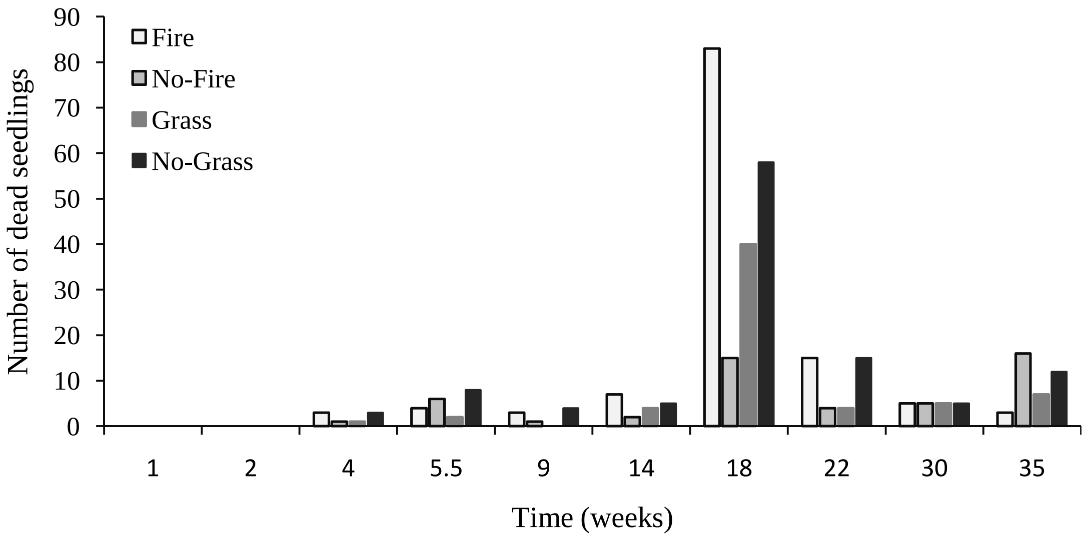


Figure 2. Change in mortality of *Acacia sieberiana* seedlings over the growing season (from 15th October to 15th June 2010) for two treatments, *Fire* and *Grass*.

3.1.2 Seed germination, seedling mortality, survival and heights during the first growing season (2009-2010)

The mean germination for all treatments at the end of the growing season reached 10.3 %; 78.1 % of those germinated seeds survived until June 2010. All four treatments significantly affected germination of *A. sieberiana* seeds over the season (Fig. 3). *Fire* increased germination by 3.6 % (z=-4.01, p<0.0001) while *Grass* (z=-6.63, p<0.0001), *Transit* (z=-6.22, p<0.0001) and *Dung* (z=3.28, p=0.001) decreased germination of *A. sieberiana* seeds by 9.4 %, 8 % and 4 %, respectively. One interaction was significant: *GrassXTransit* (z=2.72, p=0.006) showing that grass had a stronger (negative) impact on germination for *Transit* seeds, decreasing germination by 76.4 % (relative to the *No-Grass* treatment) *versus* by 55.9 % for *No-Transit* seeds.

Seedling mortality during the first growing season was significantly affected by *Fire* (z=-2.9, p=0.003) and *Transit* treatments (z=-2.73, p=0.006). *Fire* increased mortality by 11.1 % while *Transit* decreased mortality by 5.3 %. Three nested factors were significant (Fig. 4): *Fire*{*Grass}* (z=-2.5, p=0.012), *Fire*{*Transit}* (z=2.76, p=0.005) and *Fire*{*Dung}* (z=2.28, p=0.022). *Grass* significantly increased mortality but only in unburnt plots while *Transit* significantly decreased mortality only in burnt plots and *Dung* significantly decreased mortality only in unburnt plots (Fig. 4).

Seedling survival (= germination – seedling mortality) was not significantly affected by *Fire*, while *Grass* (z=7.17, p=<0.001), *Transit* (z=-4.15, p=<0.001) and *Dung* (z=3.69, p=<0.001) significantly decreased survival. The nested *Fire*{*Transit}* effect was significant (z=-4.24, p=0.002) and showed that *Transit* decreased seedling survival more in unburnt plots (from 5.54 % of survival for *No-Transit* seeds to 1.61 % for *Transit* seeds) than in burnt plots (from 5.39 % of survival for *No-Transit* seeds to 3.51 % for *Transit* seeds). The *Transit*X*Grass* interaction was also significant (z=2.40, p=0.016) and showed that *Grass* decreased seedling survival more for *No-Transit* seeds (from 7.91 % for *No-Grass* to 3.02 % for *Grass*) than for *Transit* seeds (from 4.22 % for *No-Grass* to 0.91 % for *Grass*).

Seedling height was affected by three of the four factors (Fig. 5). *Fire* (χ^2=16.64, p<0.001) and *Transit* (F-T: χ^2=27.12, p<0.001; NF-T: χ^2=5.00, p=0.025) significantly decreased seedling height (*Fire*= 11.59 ±5.00 cm, *No-fire*= 13.71 ±6.48 cm, *Transit*= 10.62 ±5.31 cm, *No-transit*= 13.47 ±5.84 cm) while *Grass* (F-G: χ^2=22.88, p<0.001; NF-G: χ^2=52.28, p<0.001) had the opposite effect (*Grass*= 15.58 ±6.33 cm, *No-grass*= 11.46 ±5.22 cm).

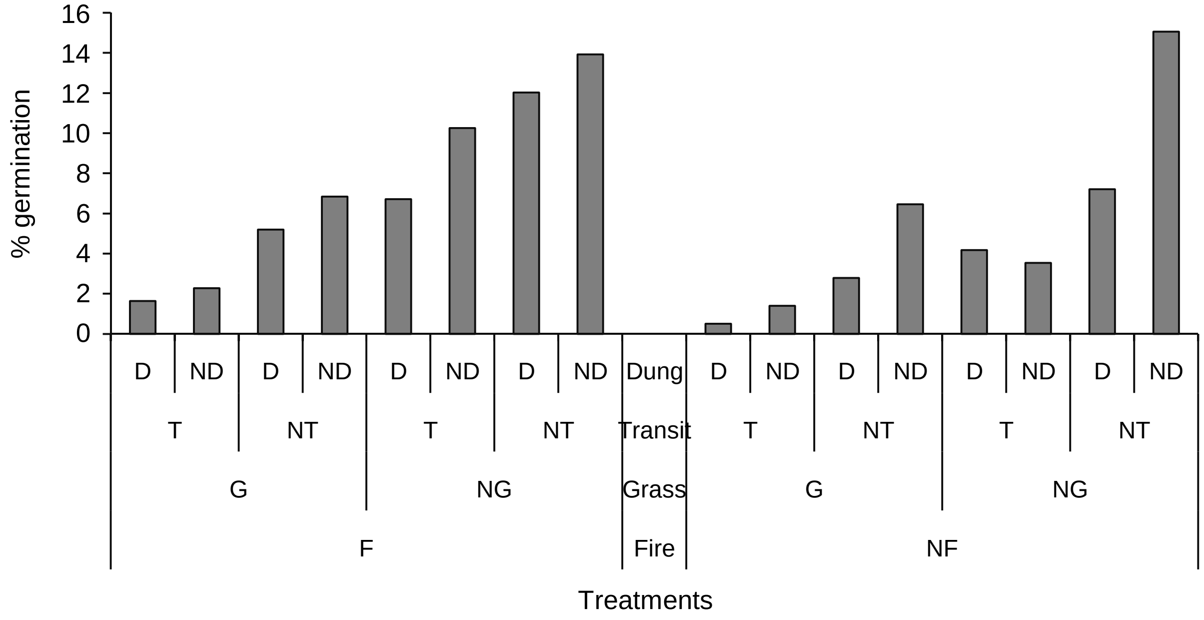


Figure 3. Comparison of *A. sieberiana* seed germination among the four treatments for the first growing season. All treatments had significant effects. F=fire, NF=no fire, G=grass, NG=no grass, T=transit, NT=no transit, D=dung, ND=no dung.

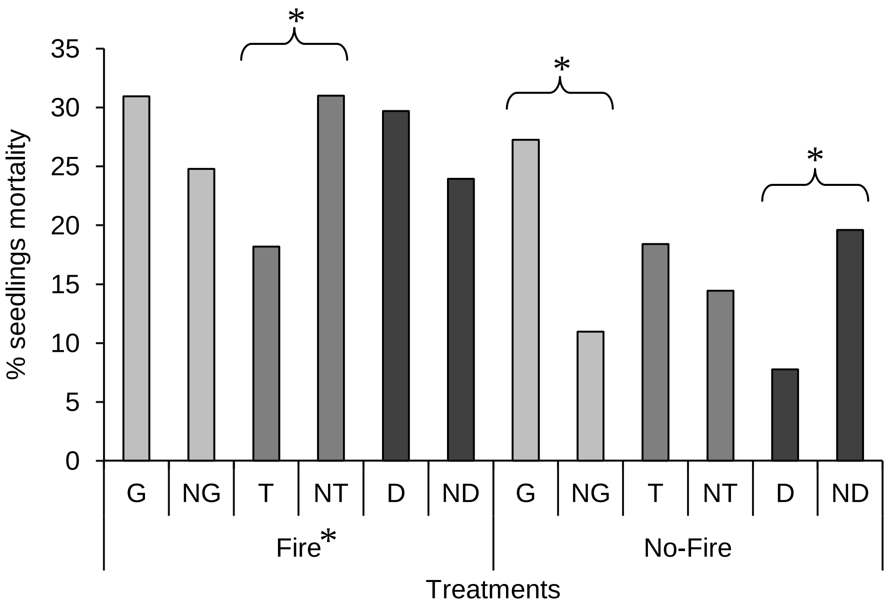


Figure 4. Comparison of *A. sieberiana* seedling mortality among the four treatments for the first growing season. G=grass, NG=no grass, T=transit, NT=no transit, D=dung, ND=no dung. Stars indicate significant differences.

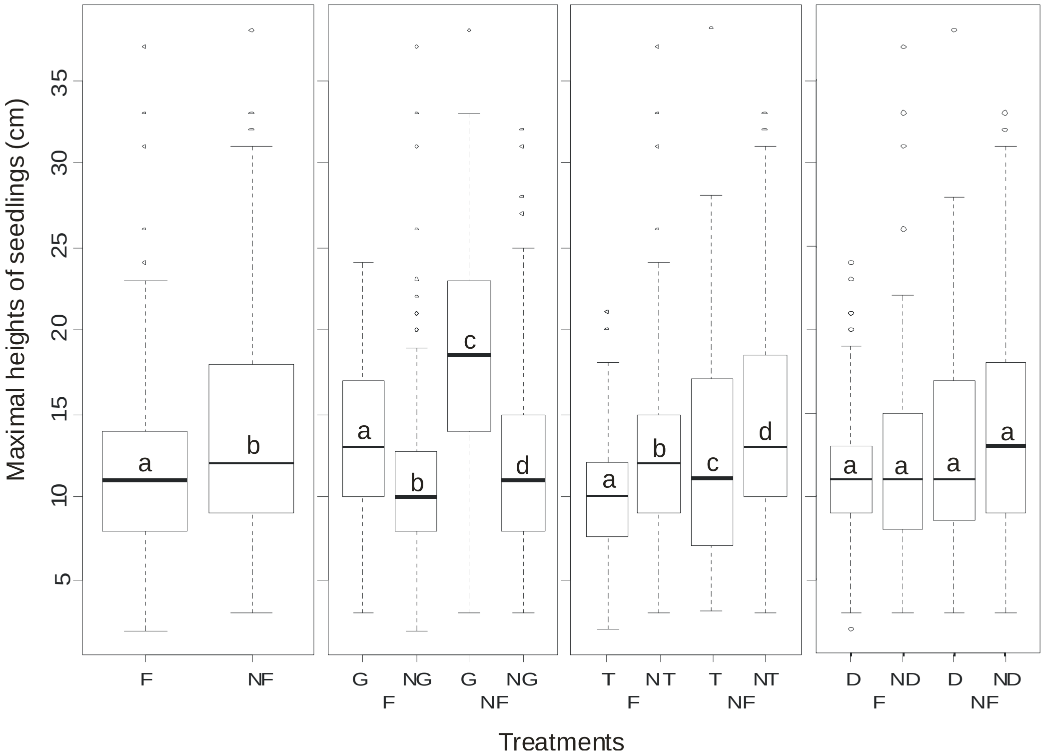


Figure 5. Box and whiskers comparison of median maximal heights of *A. sieberiana* seedlings among the treatments during the first growing season (until June 2010). F=fire, NF=no fire, G=grass, NG=no grass, T=transit, NT=no transit, D=dung, ND=no dung. Different letters indicate significant differences.

3.1.3 Seed recruitment after the dry season (November 2010)

In November 2010, after one dry season and a fire (only in the burnt plots), only 16 seeds had germinated (since June 2010) out of ungerminated 7070 seeds. There was no significant effect of treatment due to the low number of germinated seeds. Thus, results for mortality and survival were very similar. We only present results for seedling survival (Fig. 6 and 7). After the dry season, 40.6 % of the seedlings that were still alive at the end of the preceding year survived on average for all treatments. All four treatments significantly negatively affected the survival of these seedlings (*Fire:* z=-5.19, p=<0.001, *Grass:* z=-3.86, p=<0.001, *Transit:* z=-2.14, p=0.032, *Dung:* z=-2.34, p=0.018) (Fig. 7). The most important result showed in Fig. 6 is the highest survival value for the control treatment (*No-Fire, No-Grass*, *No-Transit*, *No-Dung*). The significant *Fire*{*Grass}* nested factor (z=2.71, p=0.006) showed that the presence of grass had a greater negative effect on seedling survival in burnt plots (decrease by 29.6 %) than in unburnt plots (decrease by 13.1 %). The significant *Transit*X*Grass* interaction (z=2.1, p=0.035) showed that grass decreased survival more for *No-Transit* seeds (by 31.7 %) than for *Transit* seeds (by 7 %).

Fire significantly affected the height of seedlings after the dry season. *Fire* was the only factor that was significant (F=13.46, p=0.001) and decreased the mean heights from 7.8 ±5.3 cm to 5.8 ±3.8 cm. The nested *Fire{Grass}* factor was also significant (F=8.25, p=0.007) and showed that the presence of grass in burnt plots decreased the mean height of seedlings from 5.9 ±3.8 cm to 3.3 ±3.2 cm while grass in unburnt plots increased seedlings' mean height from 7.3 ±5 cm to 9.7 ±5.9 cm.

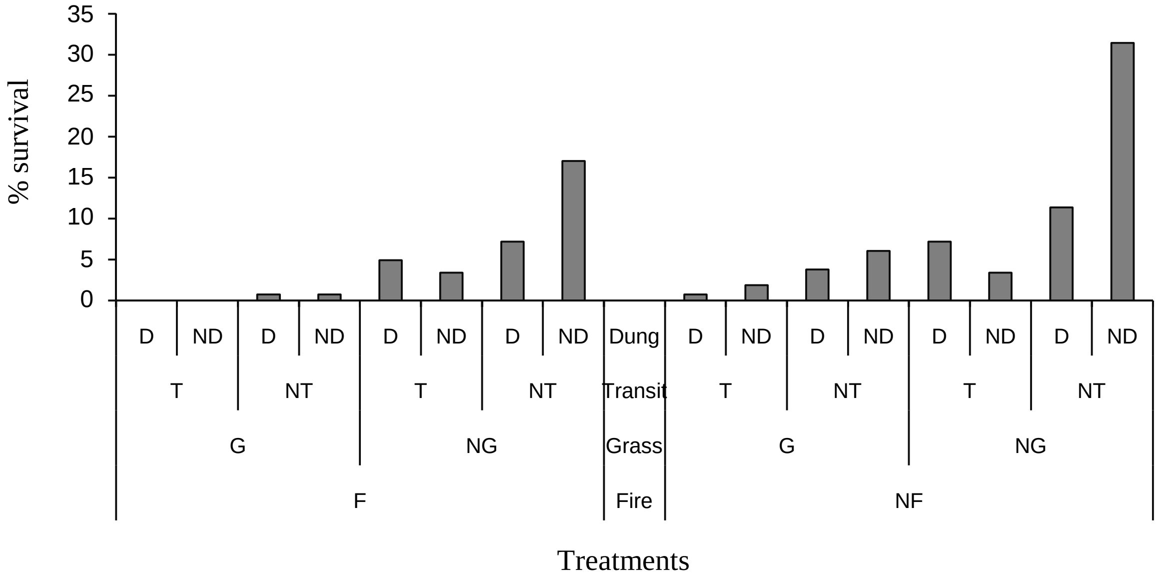


Figure 6. Comparison of *A. sieberiana* survival among the four treatments after the dry season in November 2010. All treatments had significant effects. F=fire, NF=no fire, G=grass, NG=no grass, T=transit, NT=no transit, D=dung, ND=no dung.

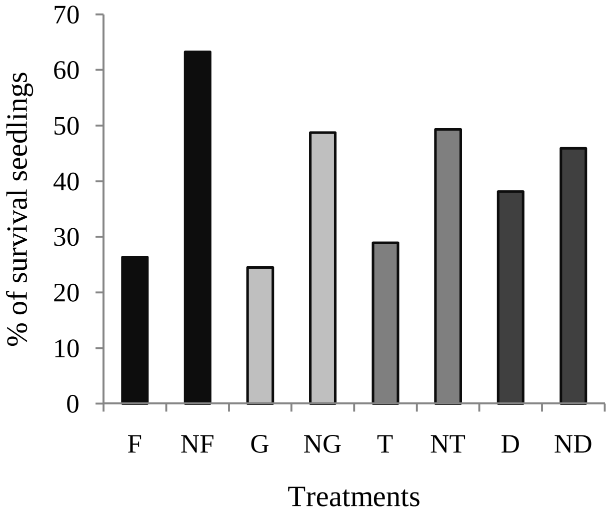


Figure 7. Comparison of *Acacia sieberiana* survival among the four treatments after one dry season in November 2010. All treatments were significant and are thus displayed. F=fire, NF=no fire, G=grass, NG=no grass, T=transit, NT=no transit, D=dung, ND=no dung.

3.2 Shadehouse experiment

The % germination during the first year of experiments reached 13.1 % on average for all treatments. *Transit* seeds were significantly different from *Control* seeds and *Acid* seeds (z=9.85, p<0.0001) (Fig. 8A). *Transit* seeds germinated more than other seeds. Surprisingly, *Acid*-treated seeds did not differ from *Control* seeds (p=0.9). The *Seeds*X*Dung* interaction was significant (z=-1.97, p=0.045) and showed that dung presence significantly increased the germination of *Transit* seeds only.

In the second year, germination was higher than during the first year: 29.2 % of seeds germinated on average for all treatments. For the two years of survey, 42.4 % of *A. sieberiana* seeds germinated. In the second year, *Dung* decreased germination (z=5.72, p<0.0001). The *Seeds* treatment was also significant (z=5.73, p<0.0001) and can be better understood considering the significant *Seeds*X*Dung* interaction (Fig. 8B): *Acid* and *Transit* seeds germinated significantly more than *Control* seeds. However, the addition of *Dung* decreased germination of *Acid* seeds and *Control* seeds but *Dung* did not significantly decrease germination of *Transit* seeds.

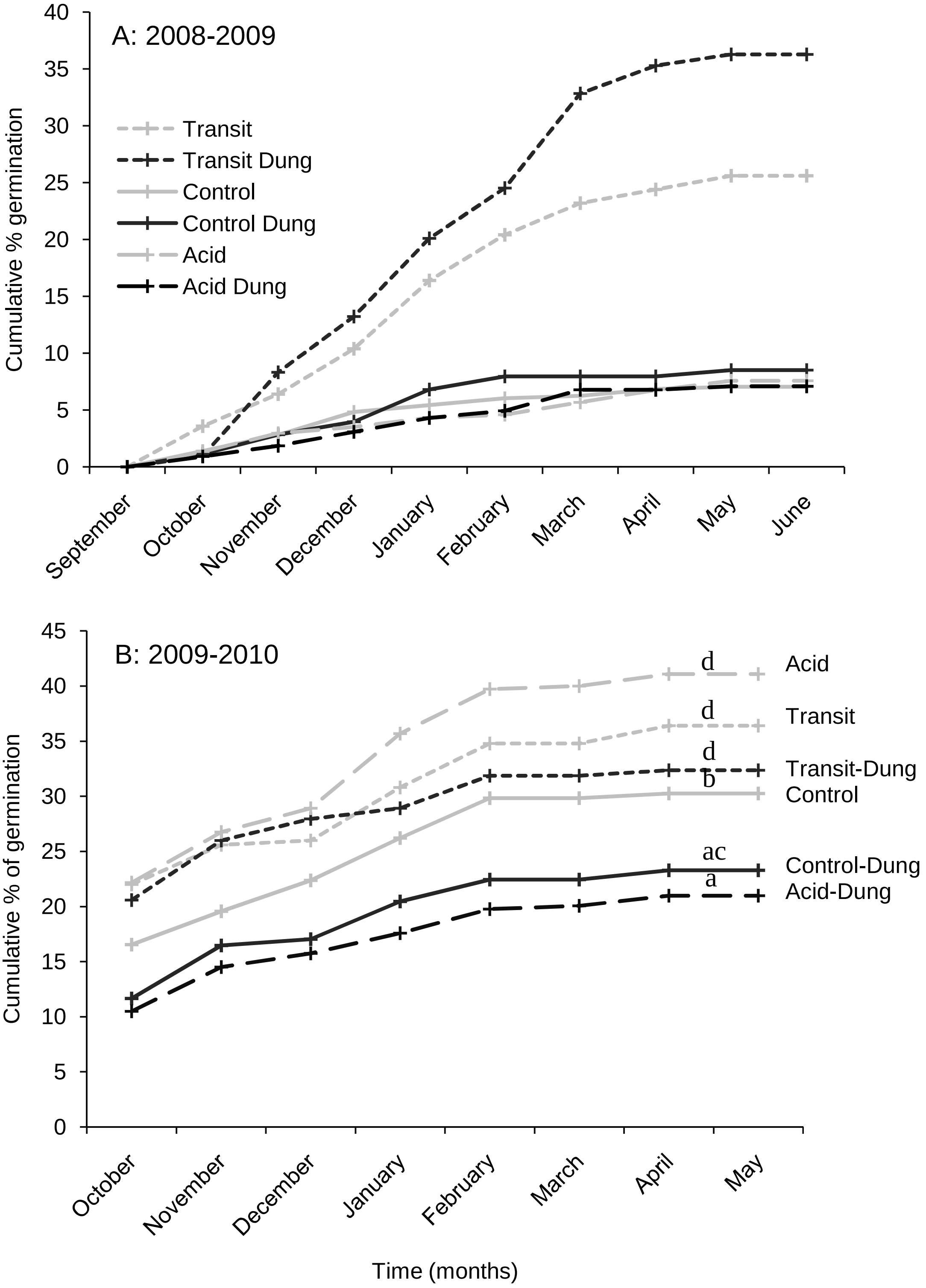


Figure 8. A) Cumulative % of germination of *A. sieberiana* seeds in the shadehouse in 2008-2009. B) Cumulative % of germination of *A. sieberiana* seeds in the shadehouse in 2009-2010. Treatments indicated in caption.

4. Discussion

4.1 General trends

A. sieberiana has been reported to germinate in the field with rates between 19 to 30 % without and with fire treatment, respectively (Mucunguzi and Oryem-Origa 1996). At the end of the growing season, our mean percentage of germination was slightly lower than those reported above but was similar for the field experiment (10.3 %) and the shadehouse experiment (13.1 %). As seed viability was good (98.7 % for *Transit* seeds and 79 % for *No-Transit* seeds), we can attribute these lower values to rainfall frequency and distribution that has been showed to particularly influence *Acacia* germination (Wilson and Witkowski 1998; Rohner and Ward 1999; Kraaij and Ward 2006). The low germination and the high mortality observed in week 18 was probably linked to the low frequency of rainfall associated with high temperatures (peak of summer season) when seedlings needed more water to develop.

4.2 Effects on *A. sieberiana* germination

The acid in the digestive tracts of cattle attacks seed coats and favors germination (Rohner and Ward 1997). This explained the higher germination for *Transit* seeds than *No-Transit* seeds in the shadehouse. Results from the field experiments lead to the opposite result. The test for seed viability in the field experiment (higher viability for *Transit* seeds than *No-Transit* seeds) should have favored higher germination for *Transit* seeds as in the shadehouse. Viability test differences may be explained by the fact that digested seeds that are infected by bruchid beetles are weakened by tunnelling larvae (Coe and Coe 1987; Or and Ward 2002). Thus, only non-infested seeds were harvested from dung and were more viable (Coe and Coe 1987; Ernst et al. 1989; Mduma et al. 2007). When clipping the seeds for viability tests, we observed a large difference in the hardness of seed coats. *Transit* seeds were much harder than *No-Transit* seeds. It has been shown that hardness of seed coats limits germination (Miller and Coe 1993). However, this does not explain why *Transit* seeds for the field experiment were harder, because we would expect the opposite to be the case due to the attack of seeds by rumen acid. Coe and Coe (1987) indicated that *Acacia* seeds do not always show a damaged coat (palisade layer) after transit. Seeds for the shadehouse experiment were directly collected from fresh dung on the farm whereas seeds for the field experiment were collected on the ground in the field. These last-mentioned seeds stayed on the ground between one to three weeks before collection. During that time they were trampled by cattle and dried by the sun. We selected 4,000 of them which were not damaged. Seeds passed through the high shearing forces of molar teeth, passed through digestive acid fluid and passed through cattle trampling. This last stage might have deteriorated the condition of seeds which were scarified by acid fluid and/or crushed by molar teeth. This process inevitably resulted in the selection of the hardest seeds.

The *Acid* treatment in the shadehouse led to a similar germination rate as the control treatment in the first year, indicating that the acid solution might not have been strong enough to attack seed coats. However, in the second year, the *Acid* treatment showed the highest germination. This means that the seed coat had been damaged enough to reduce seed dormancy, but not enough to allow germination in the first year. One year in the soil, affected by water and heat, was necessary to complete the breakage of the seed coat.

Transit seeds in the shadehouse were affected by *Dung* treatment. The germination of first year *Transit* seeds increased with *Dung*. With continuous watering during the first year, dung may favor a humid and warm environment, which is better for seed germination (Coughenour and Delting 1986; Mwalyosi 1990). Seed germination would be favored if their coats were damaged, especially in contact with soil-dung moisture, which was the case for *Transit* seeds. In the second year, dung limited germination of *Control* and *Acid* treatments although dung also did not significantly alter germination of *Transit* seeds. The decomposition of dung in the ground is usually assisted by dung beetles (Brown et al. 2010), ants, termites or other insects (Piñero and Avila 2004). The shadehouse excluded all of them so that dung decomposition was slowed. Due to the absence of watering during the dry season, dung turned into a hard, dry, waterproof layer at the soil surface (Coe and Coe 1987; pers. obs.). Hard layers are physical barriers to germination and explain why dung decreased germination in the second year.

In the field, *Grass* and *Dung* decreased germination while *Fire* increased germination. Grass and *Acacia* seeds compete for the same resources, viz. space, light, water and nutrients (Wilson 1988). At the seed stage, *Acacia* could be disadvantaged by germinating among grass (Cramer et al. 2007) due to reduced space (Coffin and Lauenroth 1990), as well as lower water and light availability (Bush and Van Auken 1995; Jeltsch et al. 1996). As *Transit* seeds were harder than *No-transit* seeds, competition with grass may be stronger, which explained that grass decreased germination more for *Transit* seeds than *No-transit* seeds. In the field, in the presence of decomposers (unlike the shadehouse), dung should be decomposed and nutrients quickly incorporated into the soil (Guillard 1967; Edwards and Aschenborn 1987). However, dung decomposition was not complete as we observed dry dung patches on the plots after a few months. As in the shadehouse, dry dung may limit seed germination due to the hard dung layer (Coe and Coe 1987) favored in the dry season when pods are available.

The positive effect of fire on germination is consistent with other studies (Du Toit 1972; Trollope 1980) but is not due to the direct effect of heat on breaking the seed coat (Babalwa and Witkowski 1997) because, in our experiment, seeds were planted after the fire. Germination on burnt plots may increase due to less dense grass cover, reducing the competition between grass and seeds for space, water (O'Connor 1995) and light (Campbell and Clarke 2006), which has been shown to increase germination.

4.3 Effects on *A. sieberiana* seedling mortality

For the first growing season, *Fire* increased mortality. Again, this result does not come from the direct effect of fire on seedlings (see above). However, annual fires for 12 years induced higher structural crust percentages on the soil surface, as was also found by Hilty et al. (2003). Crusts are known to increase runoff and limit water infiltration (Casenave and Valentin 1992; Podwojewski et al. 2011). Thus, seedlings would have less water accessible and mortality may ensue.

The dense vegetation cover in unburnt plots reduced soil detachment by dissipating the kinetic energy of raindrops. Thus, lower crust percentages occurred and allowed higher water infiltration and soil moisture (Neave and Rayburg 2007; Podwojewski et al. 2011). However, on vegetated plots, grass significantly increased mortality. We can attribute this result to above-ground light competition created by the dense vegetation cover (Kanz 2001; Campbell and Clarke 2006) and to competition for water as the seedlings grow through the grass roots. The two layer hypothesis proposed by Walter (1971) is thus not appropriate here when considering the seedling stage because grass and *Acacia* seedling roots share the same layers and compete for water and nutrients.

Dung, acting as a nutrient input (Guillard 1967; Edwards and Aschenborn 1987), decreased mortality in unburnt plots only. This result suggests that water availability was high enough to allow limitation by nutrients, unlike in burnt plots where water availability was the major constraint.

Transit seedlings had a lower mortality on burnt plots only where water was the main limitation. This indicates that seedlings emerging from *Transit* seeds may survive better with less water, linking seed quality (higher viability, harder coat) with seedling resistance. High quality seeds may have a positive impact until the seedling stage.

4.4 Effects on *A. sieberiana* seedling survival

The effect of *Fire* on survival after the first growing season was not significant, indicating that the positive effect on germination was suppressed by the negative effect on mortality. This result did not take into account the direct effect of fire in November 2010, which significantly decreased seedling survival. The heat and intensity of fire-killed seedlings has been commonly recorded (e.g. Trollope 1984; Roques et al. 2001).

Grass, *Transit* and *Dung* had the same negative effects on seedling survival in the first growing period and after the dry season. For the first growing season, *Grass* had the strongest negative effect on survival, consistent with the results of Ward and Esler (2010) and is a consequence of the germination decrease and the mortality increase with *Grass* competition. *No-Transit* seedlings were more affected by the negative *Grass* effect in the first growing season and in November 2010 probably due to the reduced ability to compete (see explanation above). The lower germination of *Transit* seeds accentuated by grass competition overrides the reduced mortality of *Transit* seeds and resulted in lower survival of *Transit* seeds, especially in unburnt plots where grass cover was denser. In November, after the dry season, *Grass* competition decreased survival more in burnt plots than in unburnt plots, because of greater competition for water due to the negative effect of structural crusts on infiltration and run-off.

Even if *Transit* and *Dung* decreased mortality during the growing season, this effect was suppressed by the strong negative effect of *Transit* and *Dung* on germination. Surprisingly, the control (*No-Dung*) had the greatest survival percentage after the dry season (Fig. 6) when there was no competition with grass and *No-Transit*, regardless of whether there was fire or not. This indicates that the main positive effect of livestock will be to disperse seeds away from the mother tree rather than the passage through the animal's gut *per se*. This favors spreading of seeds in the grassland where competition with adult trees is reduced (Miriti 2006; Kambatuku et al. 2011).

4.5 Effects on *A. sieberiana* height

The decrease in seedling height with fire during the first growing season (indirect effect) is consistent with the decrease of seedling mortality explained above. The direct effect of fire observed in November 2010 decreased seedling height as well. Seedling height was directly affected by heat (Trollope 1984; Roques et al. 2001) which reduced leaf quantity by burning and reduced post-fire regrowth.

Contrastingly, *Grass* increased seedling height for the first growing season. Other studies usually mentioned a decrease in size or biomass of seedlings with grass due to competition for water and nutrients (Wilson 1988; Kraaij and Ward 2006). Facilitation by grass could explain the results. Grass acts as a protection against high solar exposure of the day, maintaining higher soil water content (Callaway and Walker 1997). However, the negative results of grass on germination and mortality indicates that competition for light is more likely to happen than facilitation. Competition for light has been shown to be very influential when adequate water and nutrients are available (Wilson 1988). In the presence of grass, light can be a limiting factor and induce etiolation of seedlings, resulting in an increase of size (O'Connor 1995).

5. Conclusions

The results obtained in this study showed that even in a subhumid grassland (MAP = 745 mm), rainfall frequency was an important parameter controlling germination and mortality of *A. sieberiana*. Several days without rainfall during the growing season are critical to seedling establishment in the first year. After the first year, seedlings are strong enough to survive the dry season (Ward 2005). Years with frequent rainfall will thus promote higher seedling establishment than drier years. As fire has a direct negative effect on young seedlings, fire could be used especially at the end of high or frequent rainfall periods to limit tree establishment. However, the frequent use of fire can limit water infiltration and grass cover, which then increases seedling survival.

Grass competition was the main factor affecting seedling recruitment. Cattle, by reducing grass biomass promote a higher recruitment of *A. sieberiana*. Similarly, fire reduces grass biomass. In a controlled environment, cattle induced a higher germination of *A. sieberiana* through the combined effect of transit and dung. Similar results were obtained by Halevy (1974), Rohner and Ward (1999), and Bodmer and Ward (2006). Indeed, Bodmer and Ward (2006) have shown that the larger the animal ingesting the seeds, the higher the likelihood of germination. These results were all obtained under highly controlled conditions. However, in the field, the effects were opposite and the main role of cattle may be to disseminate the seeds from the mother tree. Effects of cattle are however much more complex and interactive with other factors (such as trampling and grazing of seedlings, bruchid beetle attacks on non-ingested seeds, and indirect effects of nutrient addition in dung). Further research is needed to understand the direct and indirect effects of livestock on tree encroachment.

6. Acknowledgments

We would like to thank Joe Culverwell for the use of his land. Our acknowledgments go to Moses Gichua, Andile Shange, Desale Okubamichael, Kyle Tomlinson, Gary Stafford, Lucas Janeau, Neeta Soni, and all assistants for their help in the field and in the shade house. We further acknowledge the University of KwaZulu-Natal for the facilities provided in the Ukulinga experimental farm and in the shadehouse. This study was funded by the Institute of Research and Development and by the Water Research Commission. DW acknowledges the financial support from the National Research Foundation of South Africa.

7. References

Andresen E (2001) Effects of dung presence, dung amount and secondary dispersal by dung beetles on the fate of *Micropholis guyanensis* (Sapotaceae) seeds in central Amazonia. Journal of Tropical Ecology 17:61-78

Archer S, Schimel DS, Holland EA (1995) Mechanisms of shrubland expansion: Landuse, climate or CO_2. Climate Change 29:91-95

Babalwa AM, Witkowski ETF (1997) Tolerance to soil temperatures experienced during and after the passage of fire in seeds of *Acacia karroo*, *Acacia tortilis* and *Chromolaena odorata*. South African Journal of Botany 63:421-425

Bodmer R, Ward D (2006) Frugivory in large mammalian herbivores. In: Danell K, Bergstrom R. Duncan P. Pastor J. editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, UK, Pages 232-260

Bond WJ (2008) What limits trees in C_4 grasslands and savannas? Annual Review of Ecology, Evolution and Systematics 39:641-659

Brown NAC (1965) A study of seed coat impermeability, seed germination and seedling growth in certain *Acacia* species. In: Department of pasture science. University of KwaZulu-Natal, Pietermaritzburg, South Africa, p 102

Brown J, Scholtz CH, Janeau J-L, Grellier S, Podwojewski P (2010) Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. Applied Soil Ecology 46:9-16

Burkinshaw AM, Bork EW (2009) Shrub encroachment impacts the potential for multiple use conflicts on public land. Environmental Management 44:493-504

Bush JK, Van Auken OW (1995) Woody plant growth related to planting time and clipping of a C_4 grass. Ecology 76:1603-1609

Callaway RM, Walker LR (1997) Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958-1965

Campbell ML, Clarke PJ (2006) Seed dynamics of resprouting shrubs in grassy woodlands: seed rain, predators and seed loss constrain recruitment potential. Austral Ecology 31:1016-1026

Casenave A, Valentin C (1992) A runoff capability classification system based on surface features criteria in the arid and semi-arid areas of West Africa. Journal of Hydrology 130:213-249

Coe M, Coe C (1987) Large herbivores, acacia trees and bruchid beetles. South African Journal of Science 83:624-635

Coffin DP, Lauenroth WK (1990) A gap dynamics simulation model of succession in a semi-arid grassland. Ecological Modelling 49:229-266

Coughenour MB, Detling JK (1986) *Acacia tortilis* seed germination responses to water potential and nutrients. African Journal of Ecology 24:203-205

Cramer MD, Chimphango SBM, Cauter AV, Waldram MS, Bond WJ (2007) Grass competition induces N_2 fixation in some species of African *Acacia*. Journal of Ecology 95:1123–1133

Du Toit PF (1972) *Acacia karroo* intrusion: the effect of burning and sparing. Proceedings of the Grassland Society of South Africa 7:23-27

Edwards PB, Aschenborn HH (1987) Patterns of nesting and dung burial in *Onitis* dung beetles: implications for pasture productivity and fly control. Journal of Applied Ecology 24:837-852

Ernst WHO, Tolsma DJ, Decelle JE (1989) Predation of seeds of *Acacia tortilis* by insects. Oikos 54:294-300

Gignoux J, Lahoreau G, Julliard R, Barot S (2009) Establishment and early persistence of tree seedlings in an annually burned savanna. Journal of Ecology 97:484-495

Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. Ecology 85:1555-1561

Goheen JR, Palmer TM, Keesing F, Riginos C, Young TP (2010) Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal Ecology 79:372-382

Guillard P (1967) Coprophagous beetles in pasture ecosystems. Journal of the Australian Institute of Sciences 33:30-34

Guy RM, Smith JMB (1995) A land potential classification for KwaZulu-Natal. In: KwaZulu-Natal Department of Agriculture, Cedara, South Africa

Halevy G (1974) Effects of gazelles and seed beetles (Bruchidae) on germination and establishment of *Acacia* species. Israel Journal of Botany 23:120-126

Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88:213-229

Hilty JH, Eldridge DJ, Rosentreter R, Wicklow-Howard MC (2003) Burning and seeding influence soil surface morphology in an *Artemisia* shrubland in southern Idaho. Arid Land Research and Management 17:1-11

Jeltsch F, Milton SJ, Dean WRJ, Van Rooyen N (1996) Tree spacing and coexistence in semiarid savannas. Journal of Ecology 84:583-595

Kambatuku JR, Cramer MD, Ward D (2011) Intraspecific competition between shrubs in a semi-arid savanna. Plant Ecology in press.

Kanz WA (2001) Seed and seedling dynamics of certain *Acacia* species as affected by herbivory, grass competition, fire and grazing system. Master thesis, University of KwaZulu-Natal, Pietermaritzburg, South Africa

Kraaij T, Ward D (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. Plant Ecology 186:235-246

Mbatha KR, Ward D (2010) The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. Journal of Arid Environments 74:1294-1301

Mduma SAR, Sinclair ARE, Turkington R (2007) The role of rainfall and predators in determining synchrony in reproduction of savanna trees in Serengeti National Park, Tanzania. Journal of Ecology 95:184-196

Meyer KM, Wiegand K, Ward D, Moustakas A (2007) SATCHMO: A spatial simulation model of growth, competition, and mortality in cycling savanna patches. Ecological Modelling 209:377-391

Miller MF, Coe M (1993) Is it advantageous for *Acacia* seeds to be eaten by ungulates? Oikos 66:364-368

Miriti M (2006) Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973-979

Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa

Mucunguzi P, Oryem-Origa H (1996) Effects of heat and fire on the germination of *Acacia sieberiana D.C.* and *Acacia gerrardii Benth.* in Uganda. Journal of Tropical Ecology 12:1-10

Mwalyosi RBB (1990) The dynamic ecology of *Acacia tortilis* woodland in Lake Manyara National Park, Tanzania. African Journal of Ecology 28:189-199

Neave M, Rayburg S (2007) A field investigation into the effects of progressive rainfall-induced soil seal and crust development on runoff and erosion rates: the impact of surface cover. Geomorphology 87:378-390

O'Connor TG (1995) *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. Oecologia 103:214-223

Or K, Ward D (2003) Three-way interactions between acacias, large mammalian herbivores and bruchid beetles - a review. African Journal of Ecology 41:257-265

Or K, Ward D (2007) Maternal effects on the life histories of bruchid beetles infesting *Acacia raddiana* in the Negev desert, Israel. Entomologia Experimentalis et Applicata 122:165-170

Piñero FS, Avila JM (2004) Dung-insect community composition in arid zones of south-eastern Spain. Journal of Arid Environments 56:303-327

Podwojewski P, Janeau JL, Chaplot V, Grellier S, Lorentz S (2011) Influence of vegetal soil cover on water runoff and soil detachment in a sub-humid South African degraded rangeland. Earth Surface Processes and Landforms in press

Prior LD, Murphy BP, Russell-Smith J (2009) Environmental and demographic correlates of tree recruitment and mortality in north Australian savannas. Forest Ecology and Management 257:66-74

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Ravi S, D'Odorico P, Huxman TE, Collins SL (2010) Interactions between soil erosion processes and fires: Implications for the dynamics of fertility islands. Rangeland Ecology and Management 63:267-274

Riginos C (2009) Grass competition suppresses savanna tree growth across multiple demographic stages. Ecology 90:335–340

Rohner C, Ward D (1999) Large mammalian herbivores and the conservation of arid *Acacia* stands in the Middle East. Conservation Biology 13:1162-1171

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higging SI, Roux XL, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J, Zambatis N (2005) Determinants of woody cover in African savannas. Nature 438:846-849

Sankaran M, Ratnam J, Hanan NP (2004) Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7:480-490

Scholes RJ, Archer SR (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28:517-544

Schulze RE (1997) South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria, South Africa

Smit GN (2004) An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. Journal of Environmental Management 71:179-191

Treydte AC, Heitkonig IMA, Prins HHT, Ludwig F (2007) Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology, Evolution and Systematics 8:197–205

Trollope WSW (1980) Controlling bush encroachment with fire in the savanna areas of South Africa. Proceedings of the Grassland Society of South Africa 15:173-177

Valentin C, Bresson LM (1992) Morphology, genesis and classification of soil crusts in loamy and sandy soils. Geoderma 55:225-245

Van Auken OW (2009) Causes and consequences of woody plant encroachment into western north American grasslands. Journal of Environmental Management 90:2931-2942

Walter H (1971) Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, UK

Ward D (2005) Do we understand the causes of bush encroachment in African savannas? African Journal of Range & Forage Science 22:101-105

Ward D, Esler KJ (2010) What are the effects of substrate and grass removal on recruitment of *Acacia mellifera* seedlings in a semi-arid environment? Plant Ecology in press

Wiegand K, Saltz D, Ward D (2006) A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7:229-242

Wiegand K, Ward D, Saltz D (2005) Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. Journal of Vegetation Science 16:311-320

Wigley BJ, Bond WJ, Hoffman MT (2009) Bush encroachment under three contrasting land-use practices in a mesic South African savanna. African Journal of Ecology 47:62–70

Wilson JB (1988) Shoot competition and root competition. Journal of Applied Ecology 25:279-296

Wilson TB, Witkowski ETF (1998) Water requirements for germination and early seedling establishment in four African savanna woody plant species. Journal of Arid Environnments 38:541-550

W.R.B. (1998) World reference base for soil resources. Report N°84, World Soil Resources Reports, FAO, Rome

II. Profondeur d'extraction de l'eau par les acacias au cours des saisons

Water uptake adaptations of *Acacia sieberiana* in a woody plant encroached grassland of South Africa

Séraphine Grellier[1], Jean-Louis Janeau[1], Patricia Richard[2], David Ward[3], Thierry Bariac[2], Simon Lorentz[4]

[1]IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology, Rabie Saunders Building, University of KwaZulu-Natal - Box X01 - Scottsville, 3209 South Africa
[2]BIOEMCO, Versailles-Grignon, Bâtiment Eger, 78850 Thivernal-Grignon, France
[3]School of Biological & Conservation Sciences, University of KwaZulu-Natal - Box X01 – Scottsville, 3209 South Africa
[4]School of Bioresources Engineering and Environmental Hydrology, Rabie Saunders Building, University of KwaZulu-Natal, Box X01, Scottsville, 3209 South Africa

Keywords: *Acacia sieberiana*, catena position, duplex soil, grassland, isotopes, water potential

Article in preparation for submission to Journal of Vegetation Science.

Abstract

Processes linked to woody plant encroachment in grasslands are still not understood, especially the interaction between trees and water which is one of the main drivers of encroachment. We studied the depth of water uptake of *Acacia sieberiana* of different size classes in a subhumid mountainous grassland of KwaZulu-Natal (South Africa). Water potential measurements of acacia leaves at predawn and midday were done to assess the water stress of acacias during the year. Soil samples, up to 2 m depth, and sap flow of acacias were analyzed for water isotopes ($\delta^{18}O$) along a catena in the dry and the wet seasons. Seasons, size classes of acacias as well as position in the catena did influence water potential and $\delta^{18}O$ values. Acacias were the least water stressed in September (end of the dry season-beginning of the wet season). Smaller acacias (>1 m height) were less water stressed than taller acacias (> 1 m height) which were more water demanding. Small acacias switched the dominant zone of water uptake depth from the dry to the wet season between the first 40 cm depth to deeper layers, avoiding a possible competition with grass in the wet season. Taller acacias exclusively used water sources >1 m depth except in the upper part of the catena, where the shallow water contribution by these trees was higher. Soil depth and hydraulic characteristics induced an adaptation of acacias for water uptake, which differs according to water availability (seasons) and size of acacias. These adaptations could favor encroachment in the long term.

1. Introduction

Woody plant encroachment is a world-wide phenomenon which can have important consequences on grassland properties (Grellier et al. submitted 1), soil erosion (Grellier et al. submitted 2), or tree-grass (i.e. savanna) systems (Walter 1971, Casper 1997, Eggemeyer et al. 2008) but also on off-site effects by decreasing stream water (Wilcox 2002, Huxman et al. 2005). Identifying the depth of water uptake by trees in such grasslands is essential to understand where trees will have the strongest impact in the subsurface soil compartments (McCole et al. 2007). Water availability can determine species dynamics (West et al. 2007), and is part of the larger research question on tree-grass interaction in grassland which is actively being debated (Kraaij and Ward 2006, Van Auken 2009, Grellier et al. submitted 3). Due to the dimorphic architecture of *Acacia* tree roots, with many shallow horizontal roots and a strong deep tap root (Fig. 1), this tree could potentially draw water from near-surface and deeper horizons (Schenk and Jackson 2002). Contrastingly, most grass roots have been found to be shallow (>75 % in the first 10 cm), (Weaver 1958). Even if they can penetrate deeper, sometimes as much as to 2 m depth (Weaver 1958), grass roots are mostly found in the first 30 cm (Snyman et al. 2009, February and Higgins 2010). If trees only use water from the upper layers (first 50 cm) through their shallow roots, they would compete with grass for water and grass should be favored (Belsky 1994, Daly et al. 2000). The two layer model of Walter (1971) states that trees, using deeper layers are disadvantaged compared to grass, because the grass uses the water in the uppermost layer and consequently the water is unavailable for extraction by trees from the deeper horizons. This is in contrast to naturally occuring hydrological soil processes, especially in duplex soils (Cox and McFarlane 1995) where deeper layers may be more humid than surface layers, particularly in the dry season. In this case, and because trees using deeper layers could have access to other water sources (ground water), they should be able to survive better than grass during dry periods.

We cannot easily determine the depth of water uptake from root architecture, partly because root presence does not necessarily imply water uptake (Ehleringer and Dawson 1992), and because of dimorphic tree root structures (viz. in the uppermost and deeper layers). Thus, methodologies such as those which include the use of stable isotopes have been developed to determine the water uptake depth of plants (Midwood et al. 1998, Boujamlaoui et al. 2005, Eggemeyer et al. 2008, Sher et al. 2010, Reinsch et al. in press). The ratios of the natural stable isotopes of hydrogen and oxygen in water and particularly the changes to these ratios (fractionation), can be used in this context. Fractionation is the modification of the ratio between two isotopes, for example $^{2}H/^{1}H$ and is mainly driven by two processes: 1) evaporation of soil water during which the lighter isotope is lost more rapidly than the heavier isotope. This creates a decreasing isotopic gradient from the surface to deeper layers, and 2) precipitations which has a specific signature depending on the climate (Gat 1996) and which can modify the soil water isotopic composition by mixing with soil water. Because fractionation is not modified during water uptake by vegetation, (Dawson et al. 2002), tree stem (xylem) water has the same isotopic signature as the soil water at the uptake depth and time.

Figure 1. View of an *Acacia sieberiana* on the bank of a gully showing its roots system with numerous lateral roots in the shallow soil and the strong tap root disappearing into the deeper layers.

In this study, we sampled the soil and tree stems, and analyzed the isotopic composition of the water extracted in order to determine 1) whether trees vary the depth of water uptake during two distinct seasons (September 2009 and February 2010) and 2) whether the size and the position of trees in the mountainous landscape of the studied grassland, influences water uptake. We hypothesize that smaller trees should be restricted to water extraction from shallow horizons due to their shorter roots, while taller trees should be able to draw water from both shallow and deeper horizons. Following the subsurface investigation study presented in previous chapter, spatial heterogeneity of soil properties (clay content) associated with heterogeneity of soil water availability may modify tree uptake-water depth.

Because water availability and thus plant water stress can also influence the depth of water uptake by trees (McCole et al. 2007, Eggemeyer et al. 2008), we also measured the water potential of acacia leaves. This water potential, being a consequence of the soil-plant-atmospheric continuum is a quick measure of the combined plant and soil water status (Kramer and Boyer 1995, Gebrekirstos et al. 2006).

2. Materials and methods

2.1 Description of the study site

This study was conducted in the communal grassland of the Potshini village (8km south-east of Bergville) (28º 48' 37'' S; 29º 21' 19'' E), Kwazulu-Natal province, South Africa. The altitude is between 1217 m and 1452 m. The surface area of the watershed is 2.5 km^2. The climate is subhumid, subtropical with two distinctive seasons: a rainy summer (October–April) and dry winter (May-September). The mean annual precipitation is 745 mm. The average annual temperature is 13 °C (Schulze 1997). Potential evaporation is between 1600 mm and 2000 mm (Guy and Smith 1995). Rainfall (mm), air temperature (C°) and soil temperature (C°) at 5 cm depth are shown for the study period in Fig. 2. This site belongs to the Northern KwaZulu-Natal moist grassland biome (Mucina and Rutherford 2006). Encroachment by *Acacia sieberiana* var. *woodii* (Burtt Davy) Keay & Brenan is observed in the valley. Aerial photography of our site clearly confirms woody plant encroachment over the last 30 years (Grellier et al. submitted 2) and the encroached zone represented 9.45 % of the watershed area in 2009.

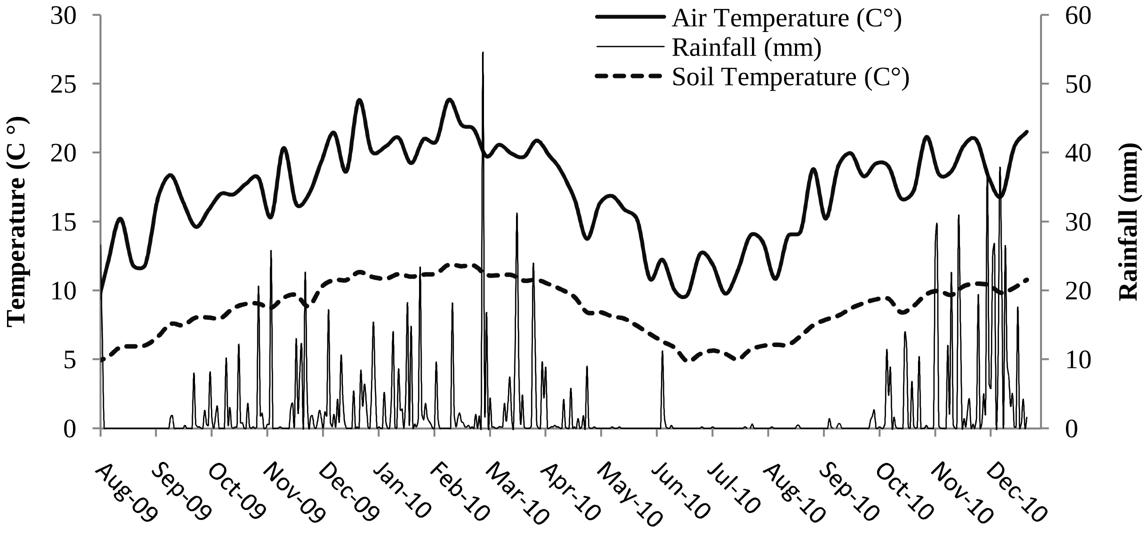


Figure 2. Meteorological data at Potshini weather station during the study period from August 2009 to December 2010. Weekly air temperature (C°), weekly soil temperature (C°), and daily rainfall (mm) are displayed.

The geology of the site is characterized by fine-grained sandstones, shales, siltstone and mudstones of the Beaufort and Ecca Groups of the Karoo Supergroup that alternate in horizontal successions (King 2002). Unconsolidated colluvial deposits from the Pleistocene fill the valleys. These soils are very prone to linear erosion in gullies, locally called “dongas” (Botha 1994, Rienks et al. 2000). Dykes of dolerite from the Jurassic, from 1 - 8 m wide intrude through the parent rock (Mucina and Rutherford 2006). The general soil type of the bottom of the watershed is luvisol (World Reference Base 1998) with two well-delimited main horizons. The A horizon is coherent, with brown color (10YR 4/1 to 10YR 4/3) and 20% clay, with many fine and medium roots. The Bt Horizon (up to 50% of clay) is dark brown, very coherent and hard with a coarse blocky structure.

Four geomorphological and ecological areas can be distinguished along the catena from the upper zone of the watershed (1452 m a.s.l.) to the lower zone (1217 m a.s.l.), where a gully is located. The very steep upper zone of the catchment (slope = 29 ±4.5 degrees) is very rocky (horizontal sandstone blocks), comprises shallow soils and supports various grass species and *Aloe ferox* (Asphodeladeae). The second zone with steep slope (17.5 ±4.5 degrees) and rocky areas (dolerites) has deeper soils and scattered *A. sieberiana* (12 acacias ha^{-1}, mainly tall acacias). The third zone of the catena with a lower slope (9.7 ±2.5 degrees) has higher *A. sieberiana* density (31 acacias ha^{-1}) than second zone with more medium-sized and small acacias. The fourth area, located at lower slope (5.9 ±1.4 degrees), has a similar soil depth than the third area and a higher density of *A. sieberiana* (60 acacias ha^{-1}) with many medium-sized and small acacias.

2.2 Experimental design

The study was carried out on three of the four geomorphological areas described above. The highest steep area was excluded as there were no acacia trees. The three other areas will be called upper, middle and lower zones according to their position in the landscape. Soil samples and acacia stems and leaves were collected in these three zones.

2.2.1 Water potential measurements

Water potential of fresh acacia leaves at predawn (3h30-5h00) and midday (11h30-13h00) were measured during three field trips: in September 2009 (beginning of the wet season), February 2010 (middle of the wet season) and June 2010 (middle of the dry season). The meteorological data for each period are presented in Table 1. Three acacias of three different size classes (0.2 m <Small<1 m, 1 m<Medium<3 m and Tall> 3 m) were randomly selected in each zone. For each acacia, three terminal freshly cut shoots were used and water potential was measured by a Scholander type pressure chamber (Scholander et al. 1965).

Table 1. Meteorological data during each sampling period of water potential measurements.

Season	**Time**	**Air Temp (C°)**	**Soil surface Temp (C°)**	**RH %**	**Solar Rad (down)**	**Rain (mm)**
Sept 2009	Predawn	11,9 ± 0,3	14,4 ± 0,3	93,5 ± 2,9	0,0 ± 0,0	0,2
	Midday	26,0 ± 2,4	18,9 ± 1,5	34,5 ± 10,4	581,9 ± 103,8	0,0
February 2010	Predawn	16,6 ± 1,1	21,2 ± 0,7	95,9 ± 0,3	0,5 ± 0,8	0,4
	Midday	30.4 ± 3,1	24,7 ± 1,7	58,9 ± 12,5	595,1 ± 150,3	0,0
June 2010	Predawn	3,3 ± 1,7	9,2 ± 0,5	83,5 ± 1,8	0,4 ± 1,3	0,0
	Midday	18,2 ± 1,3	11,8 ± 0,6	36,4 ± 6,1	459,8 ± 10,8	0,0

2.2.2 Isotope samples collection

Soil and acacia stem samples were collected in September 2009 and in February 2010 in the three zones (upper, middle and lower). The same acacias selected for water potential observation were selected for isotope analysis. Stem samples were collected with a manual corer at the base of the stem where isotopic mixing between roots and leaves is usually reduced. Each core (0.005 m diameter and 0.10-0.15 m length) was taken horizontally in the stem except for small acacias where a low branch was cut (0.10 m length). Wood heart and bark were excluded before placement in dark, capped glass bottles and stored at -25 °C until analyses. For each zone, soil samples were taken from two profiles under tall acacias (the same acacias as those selected for stem isotopes and water potential) and from two profiles outside the acacia canopy (open grassland). A manual metal corer (0.02 m diameter, 2 m length) was used to dig soil as deep as possible until an impenetrable hard layer was reached. Soil cores of 0.10 m, extracted every 0.10 m were placed immediately in dark capped glass bottles, weighed and stored at -25 °C until analysis.

Rainfall samples were collected during the rainy season of 2009-2010. Samples were collected in sealed glass bottles connected to an automatic rain gauge during each rain event. Rainfall samples were stored in a refrigerator at 3 °C until analysis.

2.3 Isotope analyses

Water was extracted from soil and acacia stem in a cryogenic vacuum extraction line (Araguas-Araguas et al. 1995, West et al. 2006) and sealed in closed glass containers. The isotopic ratio of $^{18}O/^{16}O$ was determined using a mass spectrometer. The results were reported relative to VSMOW (Vienna Standard Mean Ocean Water, Gonfiantini 1978) according to the following formula:

$\delta^{18}\text{O} = \frac{(\text{R}^{18}\text{O}_{\text{sample}} - \text{R}^{18}\text{O}_{\text{v-smow}})}{\text{R}^{18}\text{O}_{\text{v-smow}}}$ where $\text{R}^{18}\text{O}_{\text{sample}}$ and $\text{R}^{18}\text{O}_{\text{v-smow}}$ are the $^{18}\text{O}/^{16}\text{O}$ ratios for the sample and the reference V-SMOW. $^{18}\text{O}/^{16}\text{O}$ and $^{1}\text{H}/^{2}\text{H}$ isotopic ratios of rainfall samples were analyzed using a Liquid-Water Isotope Laser Analyzer (Los Gatos Research (LGR), Inc., model DLT100), calibrated against known international standards, (LGR2 (δ^{2}H -117.00, δ^{18}O -15.55), VSMOW2 (IAEA) (δ^{2}H 0.0, δ^{18}O 0.0) and IA-RO53 (IAD) (δ^{2}H -61.97, δ^{18}O -10.18). Results were also reported as delta values, expressed in parts per thousand.

2.4 Data analysis

2.4.1 Water potential

Predawn and midday leaf water potential were studied separately as two response variables. The difference between respective predawn and midday values was also calculated and called the diurnal range which indicates the range of daily relaxation (Gebrekirstos et al. 2006).

2.4.2 Isotopes

An empirical relationship exists between δ^{18}O and δ^{2}H that we can call the meteoric water line. It was first determined by Craig (1961). A global meteoric water line has been determined from the Global Network for Isotopes in Precipitation (GNIP) in collaboration with the International Atomic Energy Agency (IAEA) and the World Meteorological Organization (WMO) with samples from more than 700 stations in the world. This equation commonly used for this relationship is: $\delta^{2}\text{H} = 8 \times \delta^{18}\text{O} + 10$. For each site, a local meteorological water line (LMWL) can also be determined. The comparison between the LMWL and the GMWL helps in understanding the precipitation pathways of a given region.

Isotope signatures of tree stem (xylem) are often a mixing combination of different soil sources. In order to determine the depths of water tree uptake in the soil, mixing models can be used (Phillips and Gregg 2001, Dawson et al. 2002, Reinsch et al. in press). As we were measuring a duplex soil with two layers (A and B horizons) showing distinct isotopic signatures, a two sources model is appropriate for this area. The single isotope signature (δ^{18}O) permitted the use of a two source mixing model described by Phillips and Gregg (2001). The two sources mixing model IsoError (Phillips and Gregg 2001, version 1.04) calculates estimates and confidence intervals (95 %) of source proportional contributions to a mixture using linear mixing models and a single isotopic variable.

2.4.3 *Statistical analyses*

All statistical analyses were done in R version 2.11.1 free online software (http://www.R-project.org). The effect of *Season* (Sept 2009, Feb 2010, June 2010) on the diurnal range (difference between midday and predawn water potential) and the effect of *Season* and *Time* (Predawn, Midday) on the water potential of acacia leaves were evaluated using Kruskal-Wallis non-parametric test due to non-normality of residuals and heterogeneity of variances. As treatments were all significant ($p < 0.05$) we then analyzed the effect of *Size* (S1, S2, S3) and *Zone* (upper, middle and lower) for each season and time of day separately. We used nested ANOVA with mixed generalized linear models (GLIM) to take into account the spatial pseudoreplication of the three replicates taken for each tree. Trees were used as random factors. Normality of residuals and homogeneity of variances were tested for each model. Variables with non-normally distributed residuals or non-homogeneous variances were log-transformed, square root transformed or Box-Cox transformed. *Post hoc* t-tests with Bonferroni corrections were used to compare means between the significant factors.

$\delta^{18}O$ for acacia stems was not normally distributed and there was heterogeneity of variances. We thus used the Kruskal-Wallis non-parametric test to study the effects of *Season*, *Size* and *Zone* on $\delta^{18}O$ of acacia stems.

3. Results

3.1 Water potential

The three sampling periods (September 2009, February 2010 and June 2010) matched 1) the beginning of the wet season, 2) the middle of the wet season and 3) the middle of the dry season. Water potentials (ψ) of *A. sieberiana* leaves differed for each season (χ^2 =149.23, p<0.001), being the highest (less negative and lower stress) in September 2009 and lowest (more negative, higher stress) in June 2010. ψ also differed between predawn and midday (Sept 2009: χ^2 =83.22, p<0.001, Feb 2010: χ^2 =105.62, p<0.001, June 2010: χ^2 =27.95, p<0.001) being generally higher at predawn. We thus presented data for each season and each time period, the effect of tree size (*Tsize*) and *Zone* on water potential of acacia leaves (Table 2). The size of acacias had a significant effect (small acacias being less water stress than medium and tall acacias) in September 2009 and in February 2010 but not in June 2010 (Fig. 3). *Zone* was significant for all predawn leaf water potentials and for midday leaf water potentials in June 2010. The interaction *Tsize* X *Zone* was significant for predawn water potential in Sept 2009 and February 2010.

Table 2. Nested ANOVA results (F values and df) of mixed linear models applied on diurnal range and water potential (WP) of *A. sieberiana* leaves during the three study periods and for predawn and midday measurements. * indicates significant p values. Each model was simplified so some F values cannot be displayed (-). Three-way interaction was not significant and is thus omitted.

	Factors	*Tree Size*	*Zone*	*Tree Size* X *Zone*
Sept 2009	df	24	24	24
	Predawn WP	28.35***	23.74***	4.52*
	df	36		
	Midday WP	8.80***	-	-
	Diurnal range	-	-	-
Feb 2010	df	28	28	28
	Predawn WP	8.98**	5.32*	13.2***
	df	34		
	Midday WP	40.86***	-	-
	df	28		28
	Diurnal range	22.77***	-	3.82**
June 2010	df		31	
	Predawn WP	-	16.28***	-
	df		30	
	Midday WP	-	33.34***	-
	df		30	
	Diurnal range	-	40.55***	-

The results of June 2010 differed from the others, particularly for the middle zone of the catena which present extreme low midday water potential and extreme high predawn water potential. This may be due to manipulation error during the measurements and connection problems between the Scholander chamber and the gas bottle. Consequently, we did not take the results of the middle zone into account for the rest of the study.

Predawn measurements were higher (less negative) than midday measurements, except in June 2010 for the upper zone of the catena (Fig. 3). Predawn water potentials showed lower values (more negative) than midday water potential except again for the upper zone in June 2010. We observed a negative gradient of water potential values from small acacias to taller acacias especially at midday in September and February (Fig. 3).

The diurnal range of predawn and midday water potentials was significantly different for each season (χ^2 =51.85, $p<0.001$). In September 2009, diurnal ranges were lower than in February 2010 (Fig. 4). The diurnal range was non-significant for both *Tree Size* and *Zone* in September 2009, while in February 2010 ψ had significant lower (more negative) values for small acacias than medium and tall acacias for the middle and upper zones (Fig. 4). If we ignore the results for the middle zone in June 2010, the diurnal range values in June 2010 was very low and with high standard deviations (Fig. 4).

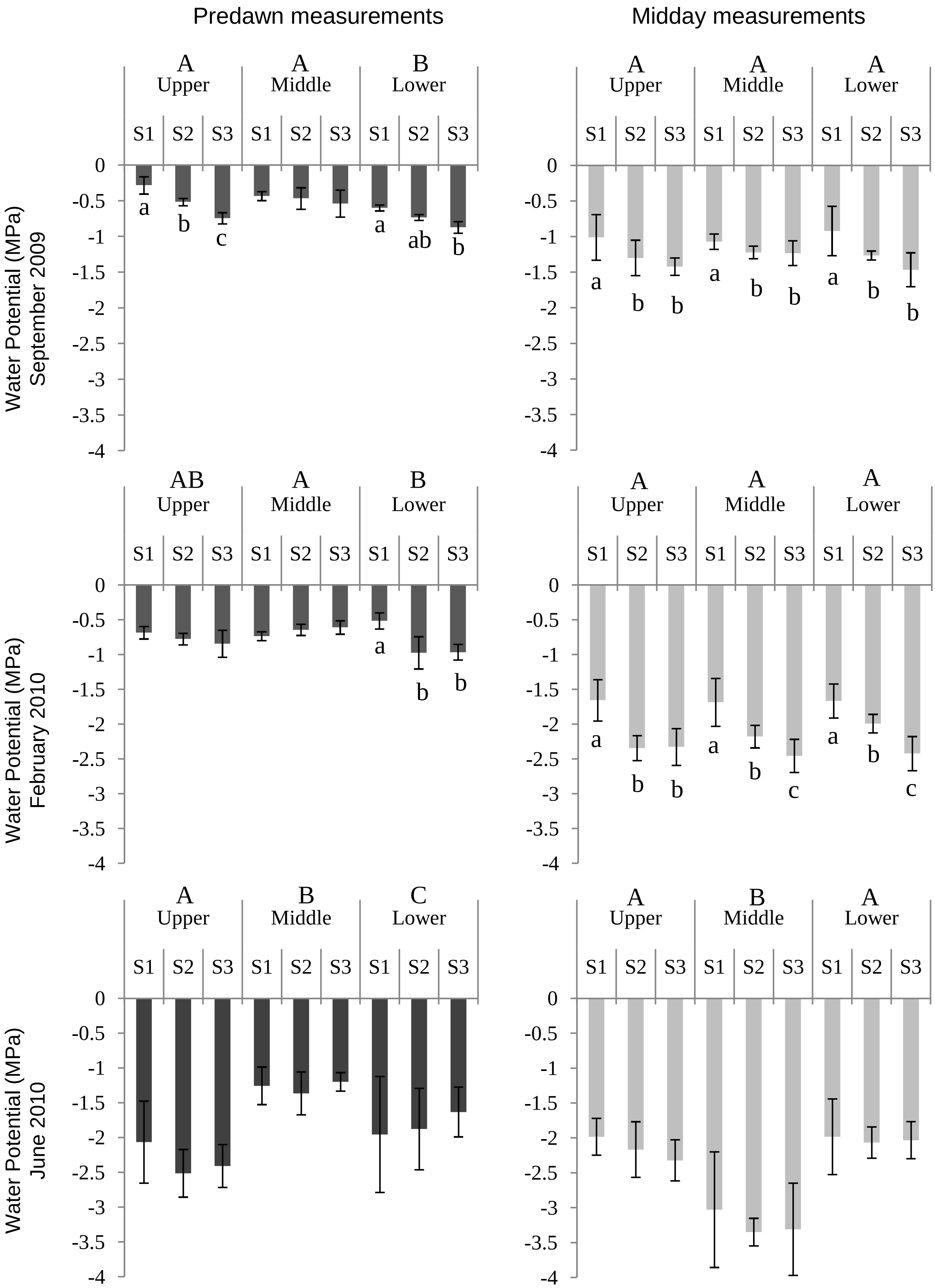


Figure 3. Water potential results of *Acacia sieberiana* leaves for the three study periods at predawn (dark grey) and midday (light grey) according to zones of the catena (upper, middle lower) and size of acacias (20 cm height<S1<1 m height, 1 m height <S2<3 m height, S3>3 m height). Different capital letters indicate significant p values between zones while different lower case letters indicate significant p values between acacia sizes ($p<0.05$). Significant differences among groups are indicated by different letters.

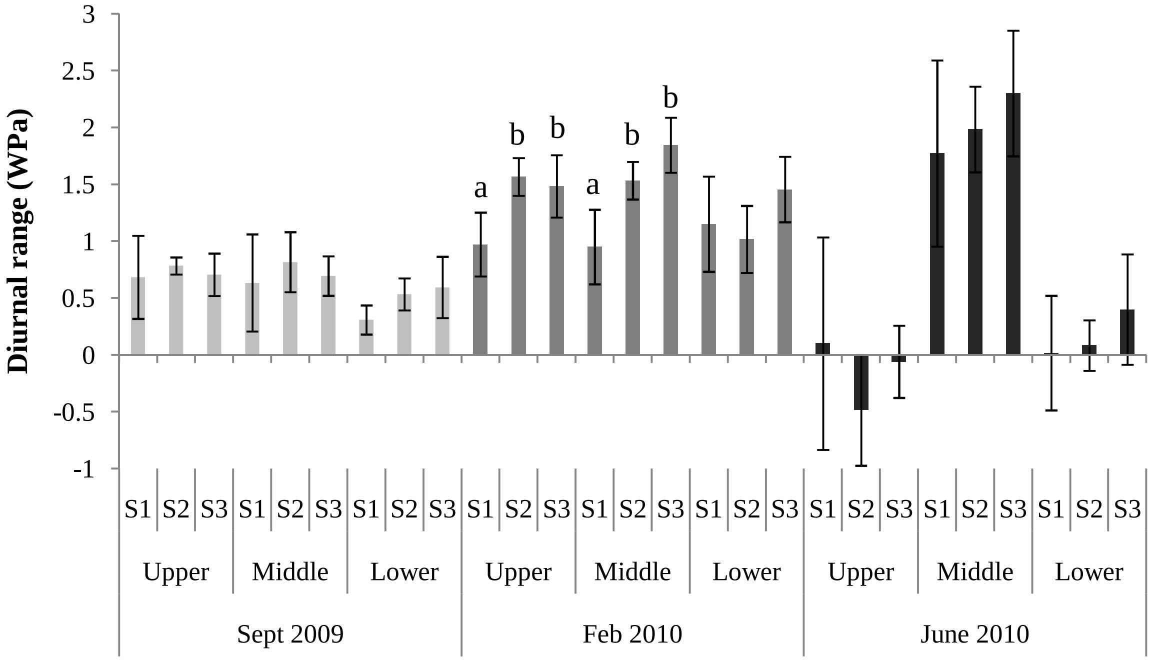


Figure 4. Means and standard deviations of diurnal range between predawn and midday water potentials of *A. sieberiana* leaves for the three study periods (September 2009, February 2010, and June 2010), for each zones in the catena (upper, middle, lower) and for the three sizes of acacias (S1= small acacias, S2= medium acacias, S3= tall acacias). Different letters indicate significant differences ($p<0.05$).

3.2 Rainfall isotopes

The high variation of $\delta^{18}O$ (from -13.03 ‰ to 1.68 ‰) was associated with a similar variation for $\delta^{2}H$ (from -87.09 ‰ to 24.28 ‰). In our study site, the intercept (15.12 ‰) of the local meteorological water line (LMWL) was higher than that of the global meteoric water line (GMWL) (10 ‰) (Fig. 5). However, the LMWL was not significantly different from the GMWL in both, slope (p=0.4) and intercept (p=0.1), (the extreme point was removed as it has a high leverage).

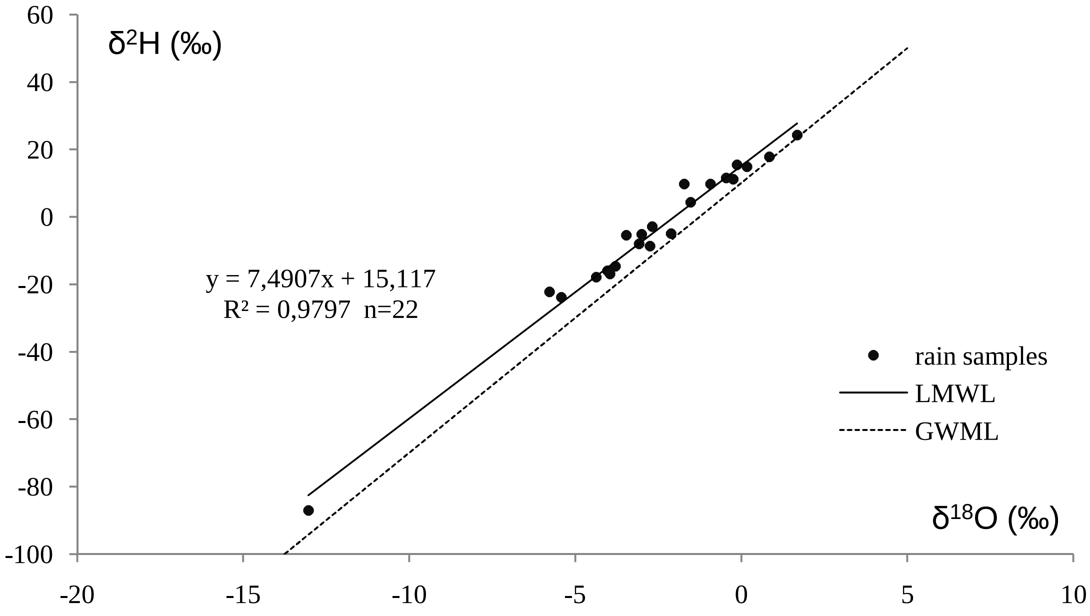


Figure 5. Isotopic values of rainfall in 2009-2010 with $\delta^{2}H$ (‰) plotted against $\delta^{18}O$ (‰). The Global Meteoric Water Line (GMWL) and the Local Meteoric Water Line (LMWL) are represented.

3.3 Soil water content and $\delta^{18}O$ isotopic composition in soil

Contrary to our expectation, soil water content did not vary significantly in all profiles between September 2009 and February 2010 (Fig. 6). The upper soil layer (0-10cm) often had higher soil water content in September than in February. Almost all profiles had a bump of soil water content in depth for both sampling periods (Fig. 6, see also Appendix 7). The lower and middle zones showed a more pronounced soil water content bump than the upper zone but the depth varied between 40 cm to 100 cm. For the middle zone, the depth of the bump was around 80 cm and matches an increase in clay and decrease in silt at similar depth on the reference soil profiles (Appendix 1). For the lower zone, the bump was located around 60 cm and matches an increase in clay and decrease in silt on the reference soil profiles (Appendix 1). For profiles taken under a canopy, soil water content was globally higher than outside canopy for the first 60 cm, especially in February.

The isotope values of $\delta^{18}O$ for all profiles had a similar trend for both sampled seasons (September and February) being higher at the surface (approaching zero or being positive) and lower deeper, close to -6 ‰ (Fig. 6). The transition between higher surface values and lower values at depth was abrupt and localized in the A horizon (0-40 cm). After 40 cm, $\delta^{18}O$ values stayed more or less constant. September 2009 and February 2010 showed a slightly different pattern especially in the A horizon: September values showed a stronger decrease than in February in the first 20 cm. This surface depletion was often stronger outside the canopy for September values.

3.4 $\delta^{18}O$ isotope values of *A. sieberiana* stems

A Kruskal-Wallis non-parametric test showed that $\delta^{18}O$ values did not differ with *Season* and *Zone*. However *Size* had a significant effect ($\chi^2 = 14.32$, $p<0.001$) with small acacias being higher than medium acacias ($p = 0.012$) and tall acacias ($p = 0.005$). This result was observed in September 2009 only (Fig. 7). Small acacias had higher values of $\delta^{18}O$ for all zones in September. This was closer to the isotope values of rainfall from the 24th of September before sampling being -3 ±0.26 ‰.

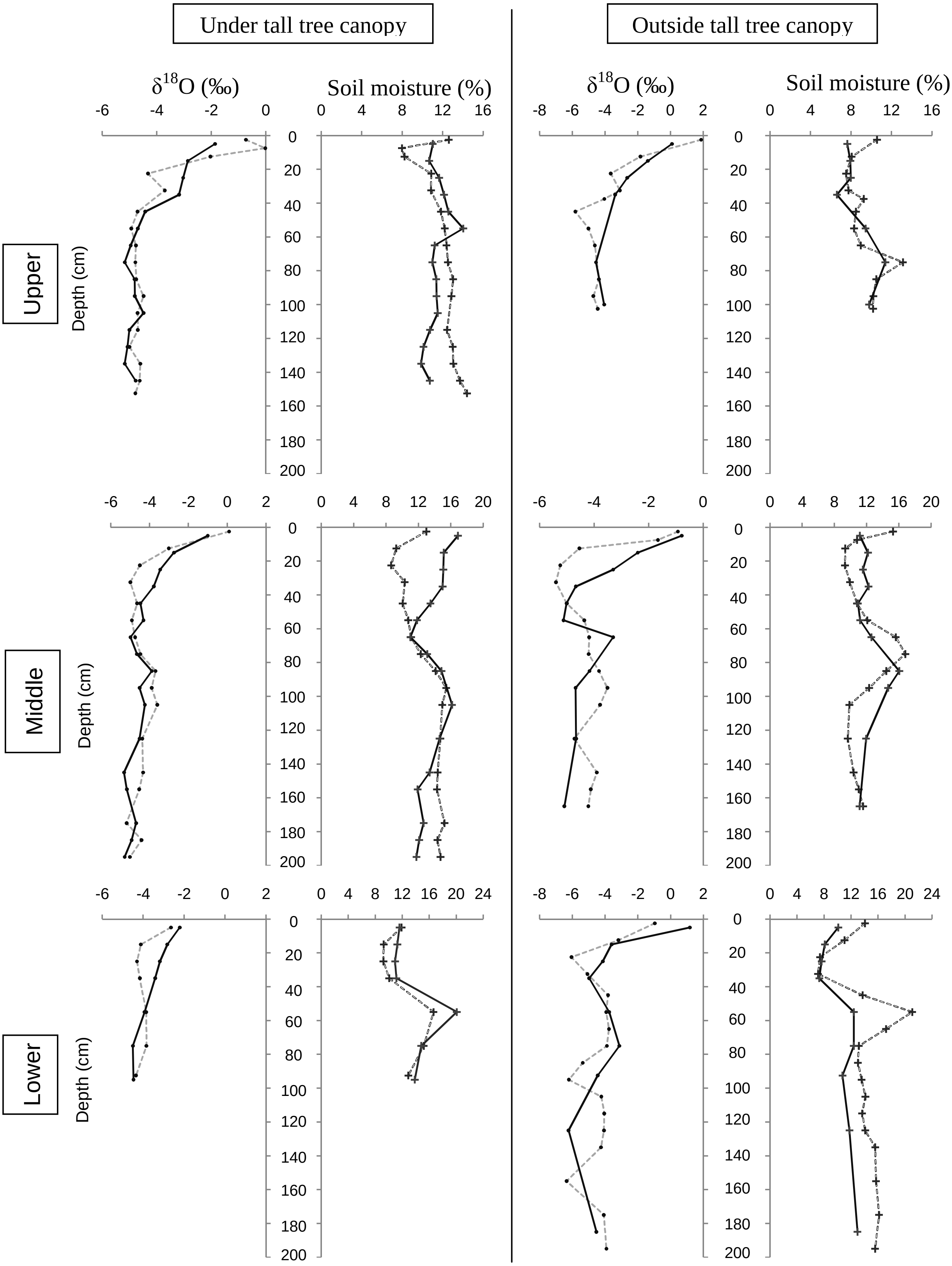


Figure 6. δ^{18}O (‰) and soil water content (%) values for each soil profile sampled under tall acacia canopy and outside canopy in the three zones in the catena (upper, middle, lower) in September 2009 (dotted lines) and in February 2010 (solid lines).

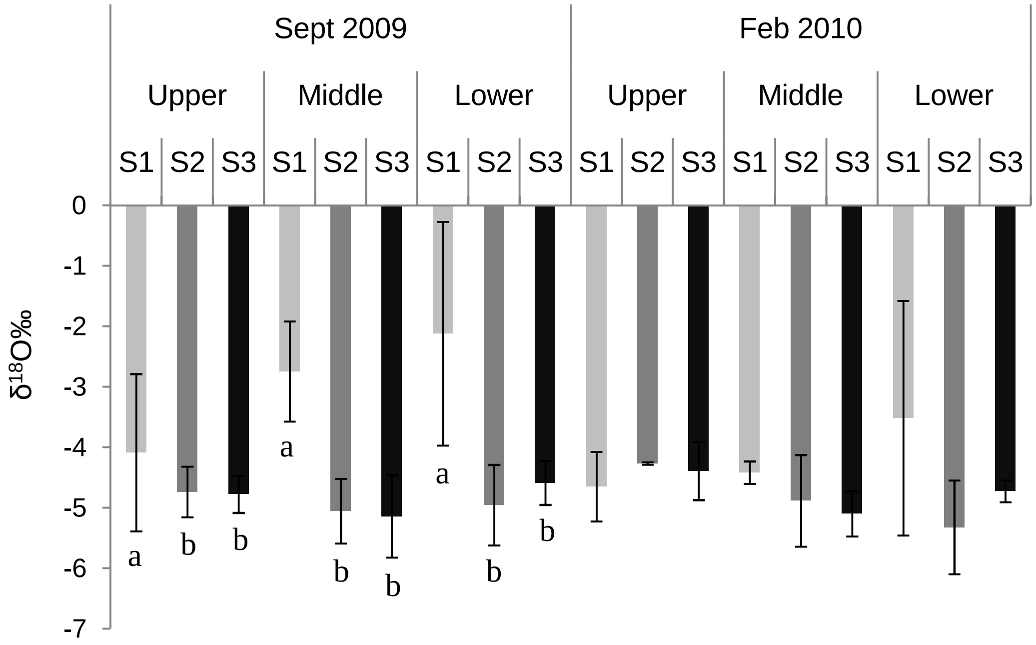


Figure 7. $\delta^{18}O$ (‰) values of *Acacia sieberiana* stems measured in September 2009 and February 2010 in the three zones of the catena and three sizes of acacias (S1 = small acacia, S2 = medium acacia, S3 = tall acacia).

3.5 Two sources mixing model results

Small acacias had similar behavior between September (end of the dry season) and February (middle of the wet season) for all zones, switching from lower layers (0-40 cm depth) to deeper layers (>40 cm depth) while tall and medium acacia sites manifested an inverse pattern in the upper zone only (Table 3). In the middle and lower zones, tall and medium-sized acacias used water mainly from the B horizon for September and February. Small acacias took up water mainly in the A horizon in September while in February they used a mixture of A and B horizon water in the lower zone and used virtually only B horizon water (92 %) in the middle zone.

The upper zone showed unique results: in September, tall and small acacias used water from both horizons with a higher proportion in the B horizon while medium acacias used B horizon water only. In February, all sizes switched: tall and medium acacias increased their fractional uptake from the A horizon to 32 ±7 % and 27 ±14 % respectively while small acacias used water from the B horizon only (Table 3).

Table 3. Two sources mixing-model applied on depth of water uptake by *A. sieberiana* in a duplex soil. Source A= A horizon (0-40cm); source B= B horizon + deeper horizons (>40cm). Three zones in the catena (upper, middle, lower) and three sizes of *Acacia* (Tall, Medium, Small) are presented for each sampling period (September 2009 and February 2010). When $\delta^{18}O$ (‰) values of acacia stem was higher than average $\delta^{18}O$ (‰) values of A horizon or lower than average $\delta^{18}O$ (‰) values of B horizon, the model was not valid (grey cells) as water uptake depth was almost exclusively done in A horizon or B horizon and deeper, respectively.

Zone	Size	Source	September 2009		February 2010	
			fraction of uptake	confidence interval	fraction of uptake	confidence interval
Upper	Tall	A	0,13 ± 0,12	0<fA<0,36	0,27 ± 0,14	0<fA<0,72
		B	0,86 ± 0,12	0,63<fB<1	0,72 ± 0,14	0,27<fB<1
	Med	A	-4,74<Horizon B values (-4,73)		0,32 ± 0,07	0,17<fA<0,48
		B			0,67 ± 0,07	0,51<fB<0,83
	Small	A	0,28 ± 0,27	0<fA<1	-4,65<Horizon B values (-4,3)	
		B	0,72 ± 0,27	0<fB<1		
Middle	Tall	A	-5,14<Horizon B values (-4,44)		-5,10<Horizon B values (-4,68)	
		B				
	Med	A	-5,05<Horizon B values (-4,44)		-4,88<Horizon B values (-4,68)	
		B				
	Small	A	-2,75>Horizon A values (-3,55)		0,08 ± 0,14	0<fA<41
		B			0,92 ± 0,14	58<fB<1
Lower	Tall	A	-4,59<Horizon B values (-4,01)		-4,73<Horizon B values (-4,3)	
		B				
	Med	A	-4,95<Horizon B values (-4,01)		-5,32<Horizon B values (-4,3)	
		B				
	Small	A	-2,12>Horizon A values (-3,82)		0,58 ± 0,91	0<fA<1
		B			0,41 ± 0,91	0<fB<1

4. Discussion

4.1 Water stress of *A. sieberiana* during the year

Water potential of leaves is an expression of plant water stress. When the plant is fully hydrated, water potential is close to zero, while under severe water stress conditions water potential usually decreases, reaching values in excess of -1.5 MPa (Shrestha et al. 2003, Bowie and Ward 2004, Gebrekirstos et al. 2006). Water potential decreased from September to June. We expected the highest values of water potential in the middle of the wet season (in February) when water availability should be the highest. However, it was in September that acacias were the least water stressed. This can be explained by 1) the small differences in soil water content measured between September and February, 2) the high February temperatures with increasing evapotranspiration and 3) acacia physiology. In February, acacias are in the middle of the reproductive period and may need more water to produce pods. The lowest values in June, the middle of the dry season, followed our expectation that in the absence of water, acacias are the most water stressed.

The higher (less negative) values of water potential measured at predawn vs. midday are in the same range as the values found by Eggemeyer et al. (2008). At predawn, in the absence of light, the plant is expected to recover from the midday stress and show higher (less negative) water potential values. However, it is not often a complete recovery because trees can transpire overnight, especially in mesic areas, where they have adequate access to water (Donovan et al. 2001). The diurnal ranges were higher in February than in September, which indicates that acacias can recover from the midday water stress more easily in February, due to higher rainfall.

Predawn water potential is considered an estimate of soil water potential (Breda et al. 1995, Sellin 1996, Donovan et al. 2001). During very dry periods, soil water decreases resulting in higher soil matrix forces, which makes the uptake of water more difficult for plants. Thus, even at predawn, water potential values can be low (Halvorson and Patten 1974, Donovan et al. 2001, Gebrekirstos et al. 2006). This is the case in June (if we exclude results from the middle zone) when the diurnal range is very close to zero. The plant fails to recover from water stress, which can lead to leaf shedding and /or decline in growth of the tree (Otieno et al. 2005). We note that the acacias in our study area lost their leaves at the end of June, a few days after our measurements.

4.2 Effects of size and position in the catena on water potential

In June 2010, all sizes of acacias did not significantly differ in their water potential. They were all water stressed and not able to recover, even at night. When results were significant (especially for midday water potential in September and February), water stress increased with acacia height class. Opposite results were expected. Due to their root architecture, taller acacias should be able to adapt their water strategies between deeper soil water and shallow soil water and thus be less water stressed than small acacias. Our results suggest that, because taller acacias have a higher demand for water than smaller acacias (through high evapotranspiration due to their large size) (Dawson 1996) they are thus more water stressed by day. However, the diurnal range of leaf water potential of taller acacias was greater than for small acacias (especially in February). This indicates that tall acacias, even if more water stressed by day, managed to recover at night. The higher (less negative) predawn water potential of smaller acacias indicates that acacias of different sizes may have access to different water sources or that smaller acacias have access to a quantity of water that is more adapted to their (reduced) requirements. This was not observed for all zones in the catena, indicating that soil water content is heterogeneous in this study area. This is commensurate with the contribution of soil water content heterogeneity to predawn disequilibrium which happens when only some roots are in wet soil and/or when hydraulic conductivity, and thus supply of water, are low (Ourcival et al. 1994, Donovan et al. 2001). Indeed, water potential measured in the lower zone differed significantly from the middle and upper zones at predawn only. Acacias had lower (more negative) water potential values at predawn in the lower zone of the catena, meaning that they found it more difficult to access water compared to other zones in the catena. The downslope areas where the soil is deeper should provide more soil water content due to topographic accumulation. This is in contradiction with the higher water stress of acacias. Greater water stress of these trees is probably due to inter-tree competition for water (Kambatuku et al. 2011), as tree density was higher in the lower zone than in the middle and upper zones of the catena.

4.3 Soil water content and isotopic soil profiles of $\delta^{18}O$

The small increase of soil water content in the first 10 cm, especially in September, may be due to the two rainfall events that happened just prior to the sampling periods. In February, this effect was less apparent because trees and grass were in their peak period of water uptake for growth and because strong evaporation occurs at the soil surface due to high temperatures in that month. Moreover, there were 7 days without rainfall before the sampling in February, causing lower soil surface water content. The rainfall water input at the soil surface is apparent in the $\delta^{18}O$ isotope profiles. The decrease of $\delta^{18}O$ from the surface to approximately 40 cm resulted mainly from evaporation processes losing lighter isotopes (Gat 1996). Evaporation processes are more active closer to the surface and increase $\delta^{18}O$ values. Below 40 cm, the soil water content increased over a specific interval in the profile in almost all profiles. This can be related to soil texture and the accumulation of clay in the B horizon. This second layer (or B horizon) may be a reserve of water for both periods, September and February. In the $\delta^{18}O$ profiles, this elevated water content does not have a specific isotope signature, except in the middle zone, outside of the tree canopies where higher values of $\delta^{18}O$

were found in the profile segment with elevated water content. It seems that this water compartment evaporated and may come from other sources than predominant vertical fluxes, such as lateral circulation due to piping (subsurface tunneling frequent in duplex soils with a dispersive C horizon) (Beckedahl 1998, Verachtert et al. 2010). Other $\delta^{18}O$ profiles show slightly decreasing $\delta^{18}O$ values to the deepest soil layer but are otherwise almost constant below 40 cm. Similar $\delta^{18}O$ profiles have been measured by Eggemeyer et al. (2008).

It is necessary to have a clear vertical gradient to be able to relate water uptake by trees to $\delta^{18}O$ profiles (Ehleringer and Dawson 1992, Brunel et al 1995). Burgess et al. (2000) worked on duplex soils such as we had in our study site and could not establish a gradient, making the use of stable isotopes less suitable for determining water uptake depth. In this study, as in Eggemeyer's study (2008), the gradient was clear enough, at least to differentiate the A horizon between 0 and approximately 40 cm and the B horizon below 40 cm depth.

4.4 Influence of size and position of acacia in the catena on water uptake

$\delta^{18}O$ values of small acacias were significantly different from those of taller acacias at the end of the dry season-beginning of wet season in September. These results have to be interpreted taking into account $\delta^{18}O$ values of soil profiles for each size-class. Tall and medium acacias were related to "under-canopy" soil profiles while small acacias were related to "outside-canopy" soil profiles (Fig. 6).

In September, when grass is dormant, small acacias favor uptake in the A horizon. Conversely, in February, when competition with grass is stronger, small acacias eventually switched to using water from deeper layers. The upper zone of the catena produced slightly different results as small acacias favor deeper layers even in September. Nonetheless, looking closer at the $\delta^{18}O$ values of small acacias for this area (-4.09 ‰) and the corresponding $\delta^{18}O$ profiles, small acacias may take up water from the interface between the A and B horizons (40 cm) in September and clearly favored deeper layers in February (probably around 80 cm depth where soil water content increased). This indicates that roots of acacias that are 0.2-1 m tall may be as deep as 80 cm into the ground. Some acacia species can develop roots to 40 cm within 15 days of germination (Wilson and Witkowski 1998), which may indicate that a young acacia tree of one or two years growth can reach horizons under 40 cm depth. Ward and Breen (1983) showed that small acacias in the Kuiseb river basin in Namibia could follow the dropping water table and quickly create deep roots.

Medium-sized acacias had the same behavior as tall acacias. In the lower and middle zones of the catena, they exclusively used deeper layers, sometimes even deeper than the maximum depth that we sampled because $\delta^{18}O$ values were lower than the $\delta^{18}O$ values observed in the B horizon. In this case, their numerous shallow horizontal roots were not used for water uptake primarily (Dawson and Pate 1996) and may serve as anchorage (Crook and Ennos 1996) or nutrient uptake (Cramer et al. 2009). However in the upper zone, their behavior was opposite to small acacias. They took up water mostly in deep layers in September, but in February, they switched partially to shallower layers. Species have been shown to increase layer exploration to endure water stress (Reinsch et al. in press). Soils of the upper zone are shallower than those in the middle and lower zones of the catena. Because acacias are more water stressed in February, they may need to find more water. Due to shallower soils in the upper zone, medium and tall acacias have to explore the entire soil profile to achieve the high water demand. In the middle of the wet season, water may be more available closer to the surface and acacias may try to reach these higher water potential zones (Plamboeck et al. 1999). A second explanation to the switch for shallower layers is nutrient uptake (Cramer et al. 2009). The first horizon is richer in nutrients due to organic matter decomposition. Acacias in the upper zones with a shallow soil may have to switch to the upper layer during growth periods to find nutrients. Nutrient uptake is associated with water uptake and may influence isotope measurements (Cramer et al. 2009). In the middle and lower zones, this switch to shallower layers did not happen when we sampled by day. Deeper soils should provide higher water content. However, at predawn we saw that acacias in the lower zone recovered less than in the middle and upper zone (*cf.* lower (more negative) water potential Fig. 3 in the lower zone). This suggests that nocturnal transpiration may occur and this may be controlled by nutrient uptake (Cramer et al. 2009), which can differ depending on nutrient availability (Scholz et al. 2007). We thus propose two possible adaptations of acacias in this ecosystem: in the upper zone of the catena, taller acacias use more soil layers by day, including shallower layers richer in nutrients. In the lower zone, taller acacias exclusively use deeper soil horizons by day but may switch to shallower layers by night for nutrient uptake (we cannot confirm this because we did not sample stems for isotopes at night).

5. Conclusions

Water uptake by grass roots usually mainly occurs in the first 30-40 cm depth (Snyman 2009, Kambatuku et al. submitted). If we consider this result for our study site, small acacias compete directly with grass for water, but they were flexible in the depth of water uptake, especially in the wet season when grass cover was dense. To avoid competition with grass, they may quickly develop deep roots, allowing deeper water uptake. Depth of soil linked to position in the catena was an important parameter impacting behavior of medium and tall acacias that were the most stressed and had the highest water demand. However, they did not compete directly with grass for water as they were able to take up water from deeper layers (see also Kambatuku et al. 2011, submitted).

A. sieberiana encroaching this grassland are thus able to adapt their water strategies. This can have direct implications on woody plant encroachment in grassland. Indigenous acacias, by adapting their water uptake strategies at a young stage may favor their establishment and increase their probability of becoming adults.

6. Acknowledgements

We acknowledge the University of KwaZulu-Natal for the facilities provided in the laboratory and the loan equipment. We also acknowledge the Bioemco team of the Center Versailles-Grignon laboratory for its contribution to the isotopic analyses of soil and trees. We also would like to thank all students and field assistants who participate to this study, especially Pauline Ferry, Gonca Okay and Sibonelo Mabaso. We further thank all Potshini Community for its support and for allowing us to work on its grassland. This study was funded by the Institute of Research and Development and by the SAFEWater project of the South African National Research Foundation (NRF), administered by the Water Research Commission, Pretoria, South Africa.

7. References

Araguas-Araguas L, Rozanski K, Gonfiantini R, Louvat D. 1995. Isotope effects accompanying vaccum extraction of soil water for stable isotope analyses. *Journal of Hydrology* 168: 159-171.

Belsky AJ. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922-932.

Beckedahl HR. 1998. Subsurface soil erosion phenomena in South Africa. Justus Perthes Verlag Gotha, Germany.

Botha GA, Wintle AG, Vogel JC. 1994. Episodic late Quaternary palaeogully erosion in northern KwaZulu-Natal, South Africa. *Catena* 23: 327-340.

Boujamlaoui Z, Bariac T, Biron P, Canale L, Richard P. 2005. Profondeur d’extraction racinaire et signature isotopique de l’eau prélevée par les racines des couverts végétaux. *Comptes Rendus Geosciences* 337: 589-598.

Bowie M, Ward D. 2004. Water and nutrient status of the mistletoe *Plicosepalus acaciae* parasitic on isolated Negev Desert populations of *Acacia raddiana* differing in level of mortality. *Journal of Arid Environments* 56: 487-508.

Breda N, Granier A, Barataud F, Moyne C. 1995. Soil water dynamics in an oak stand. 1. Soil moisture, water potentials and water uptake by roots. *Plant Soil and Tillage Research* 172: 17-27.

Brunel JP, Walker GR, Kennett-Smith AK. 1995. Field validation of isotopic procedures for determining sources of water used by plants in a semi-arid environment. *Journal of Hydrology* 167: 351-368.

Burgess SSO, Adams MA, Turner NC, Ward B. 2000. Characterisation of hydrogen isotope profiles in an agroforestry system: implications for tracing water sources of trees. *Agricultural Water Management* 45: 229-241.

Casper BB. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 545-570.

Cox JW, McFarlane DJ. 1995. The causes of waterlogging in shallow soils and their drainage in southwestern Australia. *Journal of Hydrology* 167:175-194.

Craig H. 1961. Isotopic variations in meteoric waters. *Science* 133: 1702-1703.

Cramer MD, Hawkins H-J, Verboom GA. 2009. The importance of nutritional regulation of plant water flux. *Oecologia* 161: 15-24.

Crook MJ, Ennos AR. 1996. The anchorage mechanics of deep rooted larch, *Larix europea* x *L japonica*. *Journal of Experimental Botany* 47: 1509-1517.

Daly C, Bachelet D, Lenihan JM, Neilson RP, Parton W, Ojima D. 2000. Dynamic simulation of tree-grass interactions for global change studies. *Ecological Applications* 10: 449-469.

Dawson TE. 1996. Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: The roles of tree size and hydraulic lift. *Tree Physiology* 16: 263-272.

Dawson TE, Pate JS. 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* 107: 13-20.

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP. 2002. Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics* 33: 507-559.

Donovan L, Linton MJ, Richards JH. 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well watered conditions. *Oecologia* 129: 328-335.

Eggemeyer KD, Awada T, Harvey EF, Wedin DA, Zhou X, Zanner WC. 2008. Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C_4 grasses in a semi-arid grassland. *Tree Physiology* 29: 157-169.

Ehleringer JR, Dawson TE. 1992. Water uptake by plants: perspectives from stable isotope composition. *Plant Cell & Environment* 15: 1073-1082.

February EC, Higgins SI. 2010. The distribution of tree and grass roots in savannas in relation to soil nitrogen and water. *South African Journal of Botany* 76: 517-523.

Gat JR. 1996. Oxygen and hydrogen isotopes in the hydrologic cycle. *Annual Review of Earth and Planetary Sciences* 24: 225-262.

Gebrekirstos A, Teketay D, Fetene M, Mitlöhner R. 2006. Adaptation of five co-occurring tree and shrub species to water stress and its implication in restoration of degraded lands. *Forest Ecology and Management* 229: 259-267.

Gonfiantini R. 1978. Standards of stable isotope measurements in natural compounds. *Nature* 271: 534-536.

Grellier S, Barot S, Ward D, Janeau J-L, Podwojewski P, Lorentz S, Abbadie L, Valentin C. Inconsistent environmental impacts of tree encroachment in a South African grassland. *Journal of Environmental Management*: Submitted 1.

Grellier S, Kemp J, Florsch N, Janeau J-L, Ward D, Barot S, Podwojewski P, Lorentz S, Valentin C. A 64 year study of gully extension and woody plant encroachment in a subhumid grassland of South Africa. *Landscape Ecology*: Submitted 2.

Grellier S, Janeau J-L, Barot S, Ward D. Grass competition is more important than animal dispersal. *Oecologia*: Submitted 3.

Guy RM, Smith JMB. 1995. A land potential classification for KwaZulu-Natal. N/A/95/12, KwaZulu-Natal Department of Agriculture, Cedara, South Africa.

Halvorson WL, Patten DT. 1974. Seasonal water potential changes in Sonoran desert shrubs in relation to topography. *Ecology* 55: 173-177.

Hambrey MJ. 1974. Oxygen isotope studies at Charles Rabots Bre, Okstindan, northern Norway. *Geografiska Annaler*. Series A, Physical Geography 56:147-158.

Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB. 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86: 308-319.

Kambatuku JR, Cramer MD, Ward D. 2011. Intraspecific competition between shrubs in a semi-arid savanna. *Plant Ecology* 212:701-713.

Kambatuku JR, Cramer MD, Ward D. The neutral layer in the equilibrium model of tree-grass coexistence in savannas. *Ecohydrology*, submitted.

King GM. 2002. An explanation of the 1:500 000 general hydrogeological map. Department of Water Affairs and Forestry: Pretoria, South Africa.

Kraaij T, Ward D. 2006. Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology* 186: 235-246.

Kramer PJ, Boyer JS. 1995. Water relations of plants and soils. Academic Press: New York.

Los Gatos Research. 2007. DLT-100 Liquid-Water Isotope Analyzer Automated Injection: Manual Rev 07-C. Los Gatos Research, Mountain View, California, USA.

McCole AA, Stern LA. 2007. Seasonal water use patterns of *Juniperus ashei* on the Edwards Plateau, Texas, based on stable isotopes in water. *Journal of Hydrology* 342: 238-248.

Midwood AJ, Boutton TW, Archer SR, Watts SE. 1998. Water use by woody plants on contrasting soils in a savanna parkland: assessment with δ^2H and δ^{18}O. *Plant and Soil* 205: 13-24.

Mucina L, Rutherford MC. 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute: Pretoria, South Africa

Otieno DO, Schmidt MW, Adiku A, Tenhunen J. 2005. Physiological and morphological responses to water stress in two *Acacia* species from contrasting habitats. *Tree Physiology* 25: 361-371.

Ourcival J, Floret C, Le Floc'h E, Pontanier R. 1994. Water relations between two perennial species in the steppes of southern Tunisia. *Journal of Arid Environments* 28: 333-350.

Phillips DL, Gregg JW. 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127: 171-179.

Phillips DL, Gregg JW. 2001. Model IsoError: version 1.04 http://www.epa.gov/wed/pages/models/stableIsotopes/isotopes/isoerror1_04.htm.

Plamboeck AH, Grip H, Nygren U. 1999. A hydrological tracer study of water uptake depth in a Scots pine forest under two different water regimes. *Oecologia* 119: 452-460.

Reinsch S, Schleicher J, Trinogga J, Ward D, Wiegand K, Geilmann H, Bartram S. Differences in water uptake strategies of two competing savanna woody species. *Oecologia* in prep.

Rienks SM, Botha GA, Hughes JC. 2000. Some physical and chemical properties of sediments exposed in a gully (donga) in northern KwaZulu-Natal, South Africa and their relationship to the erodibility of the colluvial layers. *Catena* 39: 11-31.

Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90: 480-494.

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA. 1965. Sap pressure in vascular plants. *Science* 148: 339-346.

Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Miralles-Wilhelm F. 2007. Removal of nutrient limitations by long-term fertilization decreases nocturnal water loss in savanna trees. *Tree Physiology* 27: 551-559.

Schulze RE. 1997. South African atlas of agrohydrology and climatology. Water Research Commission: Pretoria, South Africa.

Sellin A. 1996. Base water potential in shoots of *Picea abies* as a characteristic of the soil water status. *Plant Soil* 184: 273-280.

Sher AA, Wiegand K, Ward D. 2010. Do *Tamarix* and *Acacia* trees compete for water in the Negev desert? *Journal of Arid Environments* 74: 338-343.

Shrestha MK, Stock WD, Ward D, Golan-Goldhirsh A. 2003. Water status of isolated Negev desert populations of *Acacia raddiana* with different mortality levels. *Plant Ecology* 168: 297-307.

Snyman HA. 2009. Root studies on grass species in a semi-arid South Africa along a soil-water gradient. *Agriculture, Ecosystems & Environment* 131: 247-254.

Van Auken OW. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management* 90: 2931-2942.

Verachtert E, Van Den Eeckhaut M, Poesen J, Deckers J. 2010. Factors controlling the spatial distribution of soil piping erosion on loess-derived soils: A case study from central Belgium. *Geomorphology* 118: 339-348.

Ward JD, Breen CM. 1983. Drought stress and the demise of *Acacia albida* along the lower Kuiseb River, Central Namib Desert: preliminary findings. *South African Journal of Science* 79: 444-447.

W.R.B. 1998. World reference base for soil resources. Report N°84, World Soil Resources Reports, FAO, Rome.

Walter H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd:Edinburgh, UK.

Weaver JE. 1958. Summary and interpretation of underground development in natural grassland communities. *Ecology Monographs* 28: 55-78.

West AG, Hultine KR, Burtch KG, Ehleringer JR. 2007. Seasonal variations in moisture use in a pinõn-juniper woodland. *Oecologia* 153: 787-798.

West AG, Patrickson SJ, Ehleringer JR. 2006. Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Communications in Mass Spectrometry* 20: 1317-1321.

Wilcox BP. 2002. Shrub control and streamflow on rangelands: a process based viewpoint. *Journal of Range Management* 55: 318-326.

Wilson TB, Witkowski ETF. 1998. Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments* 38: 541-550.

Chapitre 5. Les acacias et leurs conséquences sur un pâturage raviné

© P. Podwojewski

Impact de l'*Acacia sieberiana* sur la strate herbacée présente sous la canopée : développement d'une astéracée à fleur jaune, *Senecio inaequidens*, toxique pour les vaches et les chevaux.

Le chapitre précédent ayant apporté des réponses sur les causes ou facteurs de contrôle de l'invasion ligneuse, nous allons dans ce présent chapitre étudier les conséquences de l'invasion ligneuse dans les pâturages. En introduction, nous avons déjà évoqué les apparentes contradictions entre les différentes études concernant les conséquences positives ou négatives des arbres dans les écosystèmes pâturés. C'est en connaissant les effets de l'invasion ligneuse que l'on pourra cibler au mieux les actions éventuelles de contrôle des populations ligneuses. C'est donc dans un but de compréhension des écosystèmes envahis et de pouvoir fournir des conseils de gestion de ces écosystèmes, que ce chapitre comprend trois parties. La première porte sur l'impact que peuvent avoir ces arbres sur l'érosion en ravine à l'échelle du paysage. Elle constitue la suite de l'article présenté au chapitre 3 sur l'évolution des ravines et de l'invasion au cours des 64 dernières années. Elle est donc fondée sur les mêmes photographies aériennes. Alors que les données présentées au chapitre 3 concernaient l'ensemble du bassin versant, les travaux se concentrent ici sur 15 têtes de ravines et leur zone de drainage respective en vue d'étudier l'impact des arbres localisés dans ces surfaces particulières. Cette étude s'appuie sur d'autres facteurs de cette érosion tels que des paramètres topographiques.

Les deuxième et troisième parties de ce chapitre ont été menées à une échelle plus fine, celle de la toposéquence. L'idée principale est de déterminer les conséquences des acacias et les mécanismes associés sur les propriétés du sol et de la strate herbacée. Il est question de travailler à la fois sur le plan écologique (diversité des espèces végétales, propriétés du sol) et sur le plan agro-pastoral (qualité et quantité des espèces herbacées utilisées dans l'alimentation du bétail). Il s'agit d'une étude multi-facteurs réalisée afin de comprendre les interactions entre le bétail, les saisons, la position des acacias dans la toposéquence (notamment ceux situés dans les fonds de ravines ou ceux en amont des ravines) sur les conséquences des acacias dans cet écosystème raviné.

I. L’impact de l’invasion ligneuse sur l’érosion en ravine

A 64 year study of gully extension and woody plant encroachment in a subhumid grassland of South Africa (second part)

Séraphine Grellier(1)*, Jaco Kemp(2), Jean-Louis Janeau(1), David Ward(3), Nicolas Florsch(4),
Sébastien Barot(5), Pascal Podwojewski(1), Simon Lorentz(6), Christian Valentin(7)

[1]IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology (BEEH), Rabie Saunders Building, UKZN, Box X01, Scottsville, 3209, South Africa
[2]Department of Geography and Environmental Studies, University of Stellenbosch, Private. Bag X1, Matieland, 7602, South Africa
[3]School of Biological and Conservation Sciences, John Bews Building, UKZN, Scottsville, 3209, South Africa
[4]UMMISCO, Université Pierre et Marie Curie, 4 place Jussieu, 75005 Paris, France
[5]IRD-BIOEMCO, Site Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris cedex 05, France
[6]School of Bioresources Engineering and Environmental Hydrology (BEEH), Rabie Saunders Building, UKZN, Box X01, Scottsville, 3209, South Africa
[7]IRD-BIOEMCO, 32 av. H. Varagnat, 93143 Bondy cedex, France

Keywords: *Acacia sieberiana;* aerial photographs; erosion; piping; subsurface; tree

Submitted in a combined version with Chapter 3 part I to Landscape Ecology.

<u>Abstract</u>

Gully erosion driven by water processes is usually affected by topography, land-use change and vegetation cover. We hypothesised that trees, through their effect on overland and subsurface flow, may have a negative impact on gully extension. However, very few studies have simultaneously considered tree encroachment and gullies. We used aerial photographs to study *Acacia sieberiana* encroachment and gully erosion in a South African grassland (KwaZulu-Natal Province) for a period lasting 64 years. The extension of 15 gully heads was correlated with topographic parameters and with acacia density and canopy cover of drainage areas of each gully head. Extension of the 15 gully heads did not correlate with any of the topographic parameters linked to overland flow while a positive correlation occurred with acacia canopy area in 2009 when maximum canopy cover was reached. These results, associated with the susceptibility of this duplex soil to subsurface flow and the observation of pipe systems in the field, showed the importance of subsurface processes in this subhumid grassland and that trees can be associated with increased gully erosion.

1. Introduction

Woody encroachment in grasslands has been associated with higher intensities of inter-rill erosion in semi-arid areas (Petersen and Stringham 2008) and with higher gully extension (Martin and Morton 1993). This was claimed to be due to a higher runoff associated with reduced grass cover under trees. Muñoz-Robles et al (2010) could not show that eroded gully volume was related to woody vegetation cover in Australia. Trees can increase ecosystem evapotranspiration (Scott et al 2006), increase water infiltration by stemflow (Dunkerley 2002), possibly move water from deep soil layers to shallower and dryer soil layers by hydraulic lift (Ludwig et al 2003), and modify subsurface water flow (Liang et al 2009; Huxman et al 2005). Despite the influence of surface and subsurface water flow on gully erosion, little is known about the effects of tree encroachment on gully erosion.

The objective of this study is to analyse the main factors affecting gully head extension, including woody vegetation cover in the drainage areas of 15 selected gully heads located in an encroached grassland of South Africa.

2. Materials and methods

2.1 Study site

The study site has been described in Chapter 3 part I.

2.2 Data collection and processing

This study is based on the same aerial photographs that have been used in Chapter 3 part I. A set of 7 photographs has been processed as described in Chapter 3 to obtain six time-periods: 1945-1961, 1962-1975, 1976-1984, 1985-2000, 2001-2005, 2006-2009.

A local digital elevation model (DEM) (5 m accuracy) was created from a combination of 6000 points obtained in 2009 by a differential global positioning system (DGPS) covering half of the catchment and from pre-existing contour data from NGI.

In order to highlight a possible relationship between trees and gully extension, as well as to understand what topographic/geomorphologic parameters influence gully extension, 15 gully heads were selected in the catchment. Selection was driven by the stage of gully head. Only gully heads that had the potential to increase were chosen. Gully heads already located at the top of the catchment were excluded from the analyses. Gully length (GL), gully head area (GA), retreat length (RL, m y^{-1}) and retreat area (RA, m^2 y^{-1}) of 15 active gully heads were measured and calculated for the six above time-periods in ArcGIS 9.3. Because retreat area (RA, m^2 y^{-1}) is not independent from gully size we calculated the standardized retreat area (SRA, % y^{-1}) for each gully head for the six time-periods by the following formula:

$SRA = \frac{RA}{GA} \times 100$ where RA is the retreat area ($m^2\ y^{-1}$) and GA is the gully head area (m^2).

Archydro Tools (implemented in ArcGIS 9.3) was used to compute, drainage areas of each gully head (DA) for the six time-periods. We then measured, for the six time-periods, the density and canopy area of large trees (>15 m^2) for each drainage area, and the density and canopy area of medium trees (between 1 m^2 and 15 m^2) for each drainage area.

Others topographic factors were measured for 2009 using Arcgis 9.3 for the 15 gully heads: drainage average slope (DA slope) of each drainage area, local gully head slope (β), and Stream Power Index (SPI) of each drainage area. SPI is a measure of the erosive power of the water flowing over a specific area (Bull 1979, Moore et al 1993). In order to compare our values with those from other recent studies, we applied the formula used by Kakembo et al (2009):

$SPI = \ln(\frac{DA}{L} \times \tan(\beta))$ where β is the local head slope (degrees), DA is the drainage area of the gully head (m^2) and L is the gully length (m) delimiting DA at its lowest section (Fig. 1).

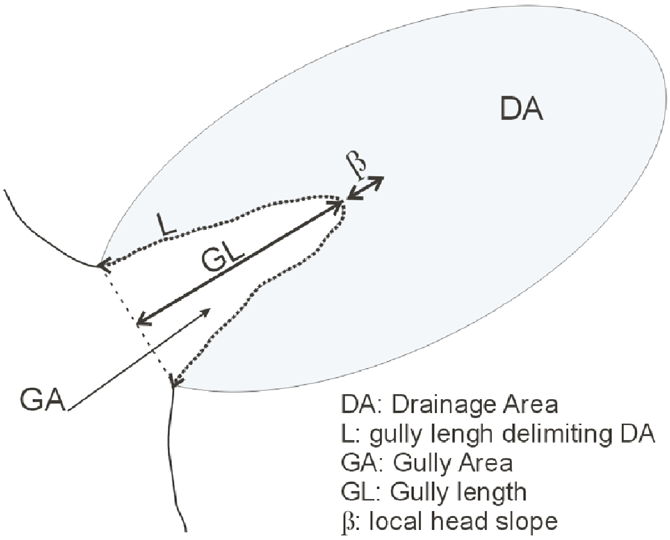


Figure 1. Representation of the parameters used in this study, especially for SPI calculation.

3. Results

The 15 gully heads presented high range of values for the different topographic parameters measured in 2009 (e.g. Table 1). Mean retreat length of the 15 gully heads varied between 0.23 m y^{-1} in 1945-1961 (data not shown) and 0.77 m y^{-1} in 2006-2009 (Table 1). One gully had a maximum retreat length in 2006-2009 of 1.67 m y^{-1} (Table 1). The mean over the 64 years period was 0.3 m y^{-1}.

Table 1. Topographic parameters measured for the 15 gully heads in 2009: drainage area (DA), drainage average slope (DA slope), local gully head slope (β), stream power index (SPI), gully length (GL), gully head area (GA). Parameters measured for the last period (2006-2009): retreat length (RL), retreat area (RA) and standardized retreat area (SRA). Mean and standard deviation (SD) are displayed.

GULLY NUMBER	DA (m^2)	DA SLOPE (degrees)	β (degrees)	SPI	GL (m)	GA (m^2)	RL (m y^{-1})	RA (m^2 y^{-1})	SRA (% y^{-1})
1	41258	15.85	9.82	3.87	120	4844	0.67	68.6	0.6
2	85597	16.40	16.75	3.79	225	11695	0.33	202.0	0.5
3	8490	6.87	5.83	3.28	98	2258	1.33	56.3	0.7
4	105150	17.17	6.94	4.08	218	8101	0.33	56.6	0.6
5	26467	10.63	3.66	2.66	143	4175	0.33	14.6	0.6
6	13054	10.63	7.36	3.01	68	875	0.33	4.0	0.6
7	17412	14.96	7.92	3.81	69	809	0.67	19.0	0.6
8	14350	10.03	5.00	3.03	71	1393	1.33	38.6	1.0
9	103776	13.59	5.73	3.84	240	12008	1.33	163.6	0.4
10	3701	7.33	4.98	2.01	65	1795	0.67	52.6	0.6
11	2790	5.22	3.06	1.21	57	555	0.33	15.0	1.1
12	57941	16.91	5.18	5.03	63	1196	1.00	33.0	0.8
13	38924	15.74	4.04	3.72	132	3585	1.67	113.0	0.7
14	9240	20.02	8.92	3.41	73	1292	0.67	43.6	0.9
15	3039	6.02	6.96	1.26	64	911	0.67	35.0	0.5
mean	35412	12.49	6.81	3.20	113	3699	0.77	61.0	0.68
SD	36336	4.69	3.34	1.05	64	3881	0.44	56.5	0.19

Correlations between retreat area (m^2 y^{-1}), gully head area (GA) and drainage area (DA) for each of the six time-periods were all significantly positive (Table 2).

Table 2. Correlations for the 15 selected gully heads (n=15) for each period between retreat area ($m^2.y^{-1}$) and the three parameters gully length (m), gully area (m^2) and drainage area (DA) (m^2).

Time periods	Retreat area /gully length		Retreat area /gully area		Retreat area /DA	
	R^2	p value	R^2	p value	R^2	p value
1945-1961	0.59	0.001	0.61	<0.001	0.54	0.001
1962-1975	0.68	<0.001	0.54	0.001	0.57	0.001
1976-1984	0.75	<0.001	0.67	<0.001	0.52	0.002
1985-2000	0.82	<0.001	0.75	<0.001	0.77	<0.001
2001-2005	0.62	<0.001	0.63	<0.001	0.48	0.004
2006-2009	0.59	0.001	0.70	<0.001	0.46	0.005

For each period, we correlated SRA (% y^{-1}) of the 15 gully heads (n=15) with measured topographic parameters and acacia population parameters. SRA did not correlate significantly with either DA or with gully head area (GA). In 2006-2009 where we could measure the different slopes on the DEM for each gully head, SRA did not correlate significantly with either DA slope (p=0.56) or with local gully head slope (p=0.62). Stream power Index (SPI) was also not significantly correlated with SRA (p=0.28).

We correlated SRA with tree density, large tree density, tree canopy area and large tree canopy area measured for each drainage area for each time-period (Fig. 2). The gully number 15 was excluded from the analyses as tree density and canopy area was extreme and pulled the results. For the first five periods, SRA was not significantly correlated with any of the previous factors. For the 2006-2009 period, SRA was significantly correlated with 3 factors (Fig. 2). Correlation with tree density was low and not significant (R^2=0.21, p=0.096). The correlation with large tree density were hardly significant (R^2=0.29, p=0.045). It was with tree canopy area (R^2 =0.46, p=0.007) and large tree canopy area (R^2=0.45, p=0.008) that the correlations were the most significant.

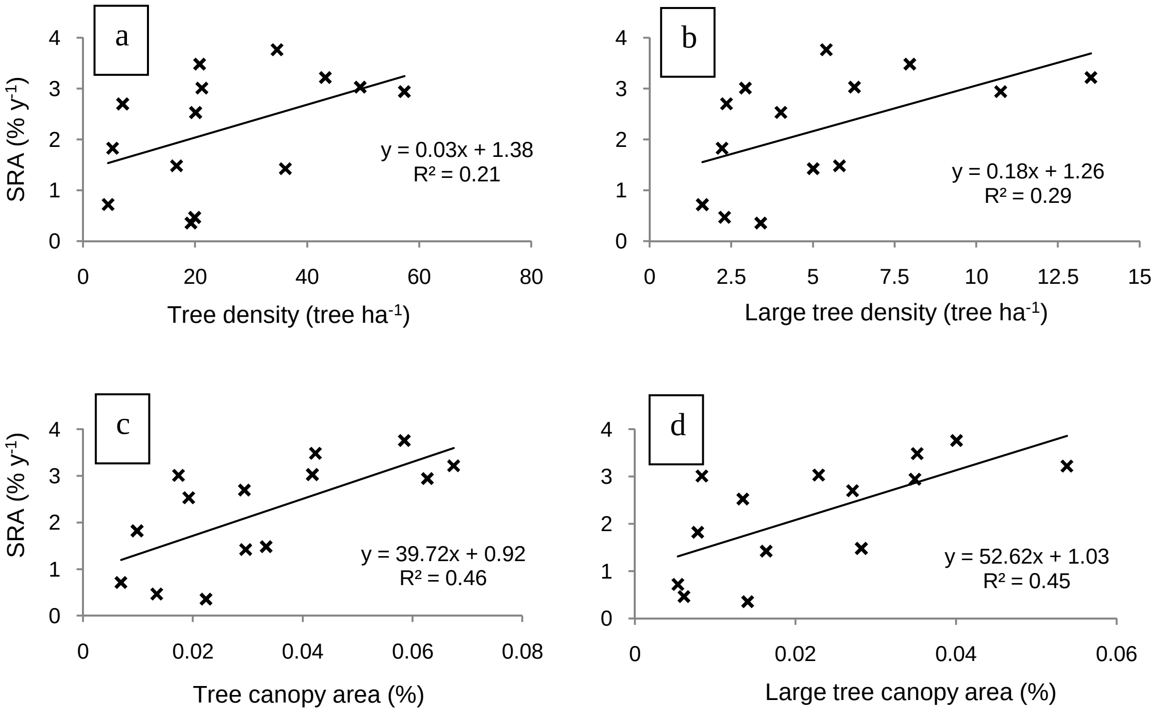


Figure 2. Linear regression relationships for the period 2006-2009 between gully standardized retreat area (SRA) of 14 gully heads and tree density (a), large tree density (b), tree canopy area (c) and large tree canopy area (d).

4. Discussion

4.1 Drivers of gully erosion, subsurface flow and piping

The retreat length of the 15 selected gully heads in this area is in the range measured in other studies. Burkard and Kostaschuk (1997) found over a period of 62 years extreme values between 0.97 and 3.64 m y^{-1} on average with a maximum at 33.39 m y^{-1}. Martínez-Casasnovas (2003) had values in the range of our study with 0.7-0.8 m y^{-1} at gully heads. Samani et al (2010) found 0.2 m y^{-1} in an arid area (Iran) whereas in Belgium (mean annual rainfall = 750 mm), Nachtergaele et al (2002) reported a mean of 1.8 m y^{-1}.

Drainage area (DA) is linked hydrologically to gully erosion as it represents the surface available for water to runoff and concentrate at a specific point where gully can be created (Schumm 1979). Correlations between retreat area (m^2 y^{-1}), gully head area (GA) and drainage area (DA) were therefore all significantly positive confirming that large gullies are growing in area at a faster rate than smaller gullies (Burkard and Kostaschuk 1997).

Whereas gully heads presented a wide range of SRA values, none of the topographic parameters could statistically explain these differences for any of the six time-periods. Drainage area, average slope of DA, local gully head slope and SPI are factors linked to drainage network and thus to overland flow. As rainfall did not vary for the 15 gully heads at each time-period (taking into account a negligible spatial variation) and considering the lack of correlations showed above, our results suggest that gully head erosion was not strongly linked to surface water runoff. This suggests that gully head erosion might be linked to other factors and processes such as subsurface water processes (Imeson and Kwaad 1980). Almost all studies related gully headcut retreat to surface runoff parameters (Poesen et al 2003; Valentin et al 2005); few studies took into account or tested subsurface hydrologic parameters. However gullies have been related to subsurface hydrology such as piping (Imeson and Kwaad 1980; Crouch 1983; Planchon et al 1987; Rienks et al 2000; Valentin et al 2005). Pipes are not always apparent on the surface and are not easy to follow or to localize and consequently to associate with gully erosion. In the study area, there was evidence of piping at different locations due to the collapse of the soil surface horizon (Fig. 3).

Pipes are specifically formed in these duplex soils due to the association of soil shrinkage inducing cracks where water concentrates, to the contrasted difference in permeability between A and B horizons (Beckedahl 1998; Verachtert et al 2010) as well as to the presence of a dispersive C horizon (Imeson and Kwaad 1980). The four pipes represented on Figure 3 are probably linked to each other and suggest that it should be subsurface water drainage to the gully. The move of the gully head erosion to upstream can be accelerated by the presence of upstream pipes in the line of the gully head (Sonnenveld et al 2005; Rienks et al 2000). Pipes can be localized and mapped from collapsed soil depressions visible from the surface (Verachtert et al 2010). The mapping of pipes that are not visible requires a methodological challenge, which was not achieved in this study. Therefore we could not test the relationship between erosion rates and pipe systems. However, field evidences and previous non-significant correlations with surface water related factors suggest that subsurface processes are more important than surface processes in this area. After Imeson and Kwaad (1980), the gully type in our landscape, which presents a typical U-shape, is associated with dispersive slope deposits and pediments, and lead to the formation of badlands.

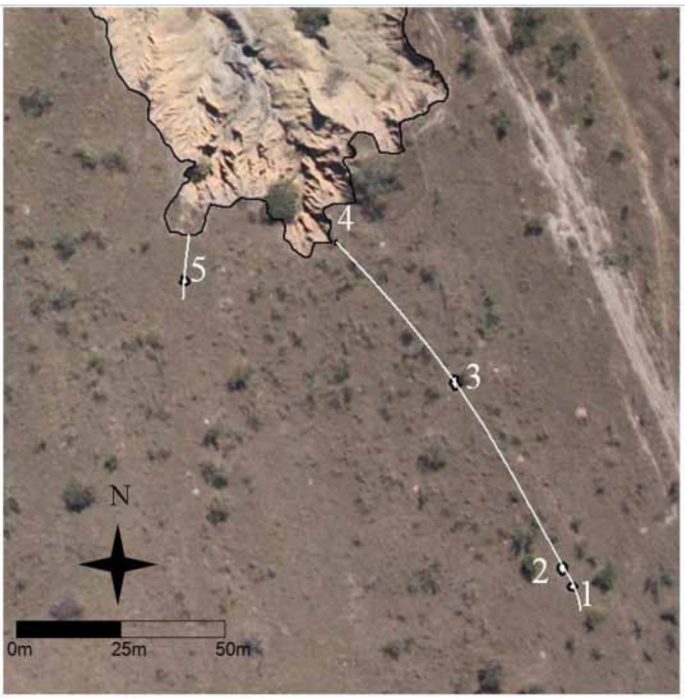


Figure 3. Aerial view of a gully head in 2009. Numbers 1 to 5 represent pipes (white circle with black perimeter) visible from the soil surface. Pipe number 4 is located at the gully head and is probably the exit of the system starting with pipe number 1.

4.2 Impact of trees on gully erosion

Correlations between SRA and tree canopy cover and tree density only started to be significant for the period 2006-2009 when a sufficient area was covered by trees. The correlation was not very high and results have to be interpreted carefully although changes from 2 % to 6 % of tree canopy area had been associated with increased SRA of gully heads from 1.8 % y^{-1} to 3 % y^{-1} (Fig. 2). In previous studies, when vegetation cover was related to gully erosion it was mainly through surface water processes: high grass cover decreases runoff and decreases gully erosion (Graf 1979; Muñoz-Roblez et al 2010). In specific areas, trees have been shown to decrease grass cover under canopy and then increase runoff (Petersen and Stringham 2008). It is however not always the case as trees can also decrease runoff through litter input which protects the soil against splash effect (Descroix et al 2001) or through the increase of under-canopy vegetation (Piersen et al 2010). A specific survey on grass cover in the study area did show that the herbaceous biomass was similar under tree canopy and in the open grassland (Grellier et al submitted). We can thus make the hypothesis that runoff should not differ significantly under canopy and outside. Surface water processes may thus not be significantly influenced by trees in this grassland. Trees have been shown to modify subsurface water (Liang et al 2009; Huxman et al 2005) and especially to increase infiltration by stemflow (Dunkerley 2002; Liang et al 2009). Stemflow infiltrates into the soil and can reach deep depth following preferentially tree roots (Martinez-Meza and Whitford 1996; Johnson and Lehmann 2006). As stemflow increases with canopy size (Martinez-Meza and Whitford 1996), sufficient tree canopy area (or tree density in a lesser extent) could favor water infiltration at the catchment scale. Sonnenveld et al (2005) mentioned that in specific cases (tunneling especially), infiltration could stimulate subsurface erosion and retreat rate of downslope gully heads. A higher amount of subsurface water may increase the swelling of clays. This may be followed by shrinkage during dry periods. Strong desiccation will create cracks and favor bank erosion from gully head walls (De Ploey 1974). Erosion rates might thus increase with higher tree canopy area through the effects of stemflow. This scenario has not been fully demonstrated in this study and needs to be further investigated.

5. Conclusions

Our results suggest that the gullies in the foothills of the Drakensberg were not primarily affected by surface runoff. The gullying process is more likely induced by subsurface runoff in this subhumid grassland.

Trees can be counter-intuitively associated to increasing gully erosion. This effect depends on tree species (architecture and characteristics) but also on the sub-canopy vegetation cover and on the drivers of erosion (surface or subsurface processes).

If the positive effect of trees on gully extension is confirmed on a larger time scale, this would have an implication in the management of grasslands where gullies are present and where tree encroachment is not controlled. Tree thinning might thus be considered.

6. Acknowledgments

The authors would like to thank the University of KwaZulu-Natal, the Institute of Research and Development (IRD), for infrastructure and financial support. We further thank the community of Potshini for sharing their land and participating to the experiment, especially Sibonelo Mabaso. A special thank go to Jean Asseline and Jean-Louis Rajot for their “pixy” experience.

7. References

Beckedahl HR (1998) Subsurface soil erosion phenomena in South Africa. Justus Perthes Verlag Gotha, Germany

Bull WB (1979) Threshold of critical power in streams. GSA Bulletin 90:453-464

Burkard MB, Kostaschuk RA (1997) Patterns and controls of gully growth along the shoreline of Lake Huron. Earth Surface Processes and Landforms 22:901-911

Crouch RJ (1983) The role of tunnel erosion in gully head progression. Journal of Soil Conservation 30:148-155

De Ploey J (1974) Mechanical properties of hillslopes and their relation to gullying in Central semi-arid Tunisia. Zeitschrift-Geomorphologie 21:177-190

Descroix L, Viramontes D, Vauclin M et al (2001) Influence of soil surface features and vegetation on runoff and erosion in the western Sierra Madre (Durango, Northwest Mexico). Catena 43:115-135

Dunkerley DL (2002) Infiltration rates and soil moisture in a groved mulga community near Alice Springs, arid central Australia: evidence for complex internal rainwater redistribution in a runoff-runon landscape. Journal of Arid Environments 51:199-219

Graf WL (1979) The development of montane arroyos and gullies. Earth Surface Processes and Landforms 4:1-14

Grellier S, Ward D, Janeau J-L et al (submitted) Inconsistent environmental impacts of tree encroachment in grassland of South Africa. Journal of Environmental Management

Huxman TE, Wilcox BP, Breshears DD et al (2005) Ecohydrological implications of woody plant encroachment. Ecology 86:308-319

Imeson AC, Kwaad FJPM (1980) Gully types and gully prediction. K.N.A.G. Geografisch Tijdschrift XIV 5:430-441

Johnson MS, Lehmann J (2006) Double-funneling of trees: stemflow and root-induced preferential flow. Ecoscience 13:324-333

Kakembo V, Xanga WW, Rowntree K (2009) Topographic thresholds in gully development on the hillslopes of communal areas in Ngqushwa local municipality, Eastern Cape, South Africa. Geomorphology 110:188-194

Liang W-L, Kosugi K, Mizuyama T (2009) A three-dimensional model of the effect of stemflow on soil water dynamics around a tree on a hillslope. Journal of Hydrology 366:62-75

Ludwig F, Dawson TE, de Kroon H et al (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. Oecologia 134:293–300

Martin S, Morton H (1993) Mesquite control increases grass density and reduces soil loss in Southern Arizona. Journal of Range Management 46:170-175

Martínez-Casasnovas JA (2003) A spatial information technology approach for the mapping and quantification of gully erosion. Catena 50:293-308

Martinez-Meza E, Whitford WG (1996) Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. Journal of Arid Environments 32:271-287

Moore ID, Gessler PE, Nielsen GA et al (1993) Soil attributes prediction using terrain analysis. Soil Science Society of America Journal 57:443–452

Muñoz-Robles C, Reid N, Frazier P et al (2010) Factors related to gully erosion in woody encroachment in south-eastern Australia. Catena 83:148-157

Nachtergaele J, Poesen J, Wijdenes DO et al (2002) Medium-term evolution of a gully developed in a loess-derived soil. Geomorphology 46:223-239

Petersen SL, Stringham TK (2008) Infiltration, runoff, and sediment yield in response to western juniper encroachment in southeast Oregon. Rangeland Ecology & Management 61:74-81

Pierson FB, Williams CJ, Kormos PR et al (2010) Hydrologic vulnerability of sagebrush steppe following pinyon and juniper encroachment. Rangeland Ecology & Management 63:614-629

Planchon O, Fritsch E, Valentin C (1987) Rill development in a wet savannah environment. Catena 8:55-70

Poesen J, Nachtergaele J, Verstraeten G et al (2003) Gully erosion and environmental change: importance and research needs. Catena 50:91-133

Rienks SM, Botha GA, Hughes JC (2000) Some physical and chemical properties of sediments exposed in a gully (donga) in northern KwaZulu-Natal, South Africa and their relationship to the erodibility of the colluvial layers. Catena 39:11-31

Samani AN, Ahmadi H, Mohammadi A et al (2010) Factors controlling gully advancement and models evaluation (Hableh Rood Basin, Iran). Water Resources Management 24:1531-1549

Schumm SA (1979) Geomorphic thresholds: the concepts and its applications. Transactions Institute of British Geographers 485-515

Scott R, Huxman TE, Williams DG et al (2006) Ecohydrological impacts of woody-plant encroachment: seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. Global Change Biology 12:311–324

Sonneveld MPW, Everson TM, Veldkamp A (2005) Multi-scale analysis of soil erosion dynamics in KwaZulu-Natal, South Africa. Land Degradation & Development 16:287–301

Valentin C, Poesen J, Li Y (2005) Gully erosion: impacts, factors and control. Catena 63:132–153

Verachtert E, Van Den Eeckhaut M, Poesen J et al (2010) Factors controlling the spatial distribution of soil piping erosion on loess-derived soils: a case study from central Belgium. Geomorphology 118:339-348

II. Impacts ambivalents de *A. sieberiana* sur les propriétés du sol et de la strate herbacée dans un pâturage sud-africain

Inconsistent environmental impacts of woody plant encroachment in a South African grassland

Séraphine Grellier[1], David Ward[2], Jean-Louis Janeau[1], Pascal Podwojewski[1], Simon Lorentz[3], Luc Abbadie[4], Christian Valentin[5], Sébastien Barot[6]

[1]*IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa*
[2]*School of Biological & Conservation Sciences, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa*
[3]*School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa*
[4]*CNRS-BIOEMCO, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France*
[5]*IRD-BIOEMCO, 32 av. H. Varagnat, 93143 Bondy cedex, France*
[6]*IRD-BIOEMCO, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France*

Keywords: *Acacia sieberiana*; grazing; herbaceous layer; *Senecio inaequidens*; soil properties

Submitted in a reduced version to Journal of Environmental Management (dry season measurements have been excluded).

Abstract

Background and aims: Woody plant encroachment in grasslands is a worldwide phenomenon. Despite many studies, its consequences on grass and soil properties are still unclear. To better understand impacts of trees on grassland properties we asked the following questions: Do trees have an impact on grass and soil properties; is the size of trees influential? Does this impact change with season (dry and wet), livestock and position of trees in a catena (from the bottom to upper parts of the catchment)?

Methods: We examined a mountainous subtropical grassland of South Africa encroached by *Acacia sieberiana* (indigenous species). Grass and non-grass species diversity, biomass, and quality as well as soil properties were studied during the dry and the wet seasons (November 2008 and April 2009).

Results: Non-grass species richness, soil moisture and soil nitrogen increased under acacias in the dry season. Non-grass species richness, grass green leaf biomass and grass leaf nitrogen increased under tall acacias in the wet season. These positive impacts were counteracted by the increase under acacias of the indigenous *Senecio inaequidens* (Asteraceae) which is toxic to horses and cattle. Season did modify tree-grass interaction favoring soil properties in the dry season. Medium-sized acacias had negative effects on grass quality in the wet season counteracted by increased soil properties in the dry season. Livestock resulted in an increase in grass quality whereas position in the catena had no effect.

Conclusions: We advise that *S. inaequidens* and *A. sieberiana* populations are controlled to avoid transformation of the grassland into woodland. Adaptive management with goats and sheep is proposed as a solution.

1. Introduction

Worldwide, grasslands account for 50 % of the earth's total land area (Asner et al., 2004); almost 40 % of the global population depend on them (Reynolds et al., 2007). Any degradation or change occurring in grasslands will have a strong impact on local human populations, especially on rural livestock-dependent communities. Woody plant encroachment in grassland is a widespread phenomenon (Wiegand et al., 2005; Bond, 2008; Graz, 2008; Van Auken, 2009), that reduces the area available for grazing. Encroachment has been observed in grasslands for at least 140 years (Mayeux et al., 1991) and has been recorded in America, Australia, Africa and Southeast Asia (Archer et al., 2001), negatively affecting 20% of the world's population (Turner et al., 1990).

The causes of woody encroachment in grassland and savannas are still debated by numerous authors and remain unclear (Ward, 2005). However, a multi-causal model combining geographic location and climate (especially mean annual precipitation) has been suggested for savannas by Sankaran et al. (2005). Climate change and especially the increase of CO_2 in the atmosphere favoring the growth of C_3 plants (Ward, 2010) as well as the possible reduction in competition for water and soil nutrients between trees and native grasses (reduced by grazing) have been reported to increase woody encroachment (Van Auken, 2009). Fire management may exacerbate woody encroachment (if bare ground is created at a suitable time for mass recruitment). Similarly, livestock may also increase the degree of encroachment by dispersing tree seeds (Van Auken, 2009).

In the last 50 years, the phenomenon of woody plant encroachment has increased, and both positive and negative effects on grassland and savanna functions and properties have been reported (Scholes and Archer, 1997; Van Auken, 2009). For example, trees increased grass matter and soil nutrients in Ethiopia (Abule et al., 2005), while they decreased grass cover and its ability to uptake carbon and nutrients in grassland of central USA (Lett and Knapp, 2003). Results are highly variable. The spatial scale of observation has been highlighted as an important factor playing a role in the controversy about impacts of tree encroachment. At the individual tree scale, positive effects on grass quality and soil nitrogen (for leguminous trees such as acacias) have usually been shown, where trees are described as "islands of fertility" (Treydte et al., 2007; Ravi et al., 2010) whereas at the landscape scale, effects on grass phosphorus and productivity were found to be negative (Riginos et al., 2009). However, this trend cannot be generalized and depends mainly on tree density (Riginos et al., 2009). Climate and especially rainfall also modify the responses of sub-canopy vegetation. In arid and semi-arid areas, water limitation occurs and trees, through shading, can have more positive impacts on the grass layer than in more humid areas (e.g. Belsky et al., 1993; Treydte et al., 2007). This is, however, not always the case (Knapp et al., 2008). Impact of trees on grassland properties in wetter areas seem to be less conspicuous or more difficult to show (Treydte et al., 2007). This study will focus on subhumid grassland in order to better understand woody plant encroachment in this climate. Grasslands are not always located in vast plains, but also in mountainous areas. Soil properties can differ along a catena (Oztas et al., 2003) and may have an impact on tree-grass interaction. This is why we integrated a spatial aspect along a catena and focused on the following questions:

Do trees have an impact on grass and soil properties?

Is the size of trees influential?

How do livestock and seasons affect tree-grass interactions?

Does the position of trees in the landscape (from upper to lower part of the catena) modify the impact of trees on grass and soil properties?

2. Materials and methods

2.1 Description of the study site

The study area is located in the Potshini village (8km south-east of Bergville) (28º 48' 37" S; 29º 21' 19" E), Kwazulu-Natal province, South Africa. The site is located in a north-sloping watershed of the Tugela basin (30,000 km²) and is representative of the KwaZulu-Natal Drakensberg foothills. The altitude is between 1217 m and 1452 m. The surface area of the studied catchment is 2.5 km^2. The climate is subhumid subtropical with two well marked seasons: rainy summer (October–April) and dry winter (May-September). The mean annual precipitation calculated from the last 65 years is 745 mm. The mean annual temperature is 13 °C (Schulze, 1997). Potential evaporation is between 1600 mm and 2000 mm (Guy and Smith, 1995). The area can be characterized as mesic. Mucina and Rutherford (2006) classified the vegetation of this site as belonging to the grassland biome, specifically the Northern KwaZulu-Natal moist grassland, which is usually dominated by *Themeda triandra* Forssk and *Hyparrhenia hirta* (L.) Stapf. Geographically, this biome is adjacent to savanna biomes. Encroachment by a single indigenous tree species, *Acacia sieberiana* var. *woodii* (Burtt Davy) Keay & Brenan, is observed in the valley. Aerial photography of our site clearly confirms tree encroachment over the last 30 years and represented 9.45 % of the watershed area in 2009 (Grellier et al submitted).

The geology of the site is characterized by fine-grained sandstones, shales, siltstone and mudstones of the Beaufort and Ecca Groups of the Karoo Supergroup that alternate in horizontal successions (King, 2002). Unconsolidated colluvial deposits from the Pleistocene fill the valleys. These soils are very prone to linear erosion in gullies, locally called “dongas” (Botha, 1994). Dykes of dolerite from the Jurassic, from 1 - 8 m wide intrude through the parent rock (Mucina and Rutherford, 2006). The general soil type of the bottom of the watershed is luvisol (World Reference Base, 1998) with two well-delimited main horizons. The A horizon (0 to 40-50 cm) is coherent, with a brown color (10YR 4/1 to 10YR 4/3) and 20% clay, with many fine and medium roots. The Bt Horizon with up to 50% of clay (from 50 cm to 100-120 cm) is dark brown, very coherent and hard with a coarse blocky structure.

Four geomorphological and ecological areas can be distinguished along the catena from the upper part of the watershed (1452 m a.s.l.) to the lower part (1217 m a.s.l.) where a gully is located. The very steep upper part of the catchment (slope = 29 ±4.5 degrees) presents a vegetation composed mainly of various grass species and *Aloe ferox*. The second part with steep slope (17.5 ±4.5 degrees) and rocky areas (dolerites) has a low acacia density (12 acacias ha^{-1}) with a majority of tall *A. sieberiana* trees. The third part in the catena with a lower slope (9.7 ±2.5 degrees) has an increasing *A. sieberiana* tree density (31 acacias ha^{-1}) with more medium-sized and small acacias. The fourth area located just upstream of a gully, with gentle slope (5.9 ±1.4 degrees), has a higher density of *A. sieberiana* trees (60 acacias ha^{-1}) with many medium-sized and small acacias.

This grassland is a communally-owned grassland belonging to the community of Potshini. Management of cattle and goats mainly follows two rotation periods: 8 months/4 months. During the maize growing season and until harvest (8 months) the cattle are kept in the grassland areas (November to June); during the winter (4 months), the cattle feed on the maize residues in the fields (July to October) located around the community settlement.

2.2 Data collection

2.2.1 Experimental design

In order to understand the impact of the seasons on the acacia-grass system, we sampled soils and vegetation during two periods of the year: at the end of dry season - beginning of wet season (November 2008) and at the end of wet season (April 2009). In 2008, the rainy season started late and November was still very dry with the first significant rains only after our first sampling.

We selected 40 acacias of two size classes, 20 tall acacias (>3 m height) and 20 medium-sized acacias (1 - 3 m height) according to their location in the catena to be equally distributed in each of the three zones. The tall acacias were on average 5.5 ± 1 m tall; they had a mean diameter at breast height of 0.33 ± 0.12 m and a canopy radius of 4.7 ± 1.8 m. The medium-sized acacias were on average 2.55 ± 0.5 m tall, with a mean diameter at breast height of 0.08 ± 0.02 m and a canopy radius of 1.61 ± 0.33 m. We selected 24 locations away from acacias and distributed in the three areas of the catena to be used as “control”, i.e. open grassland. Half of the locations for each treatment (tall acacias / medium-sized acacias / controls) were fenced in October 2008 in order to exclude livestock. For each location, one 50 X 50 cm plot (n=64) was delimited for further soil and vegetation sampling. Under acacias, these plots were centred at 50% of the canopy radius southwards where acacia effects should be the highest due to shade and north-facing orientation of the watershed (NB: southern hemisphere).

2.2.2 Vegetation collection

Within each plot, vegetation was clipped to ground level, separating all non-grass species and grass species. All non-grass species were identified. *Senecio inaequidens* DC. (Asteraceae) was treated separately from non-grass species, because this species had a very high biomass at the end of dry season-beginning of the wet season compared to other non-grass species. Its sum with other species in a global "non-grass biomass" variable masked all other non-grass species. The main grass species were identified and a visual estimation of the abundance of each species was made. The number of the main grass species and all non-grass species was determined for each quadrat to obtain grass species richness and non-grass species richness. Grass green leaf material of April 2009 samples was separated for further analyses. We could not sample enough grass green leaf material in November 2008 for chemical analyses (due to the dry season).

2.2.3 Soil collection

On the same plots, we collected soil samples at depths of 0-20 cm for analysis. The determination of soil moisture ($SW_{0\text{-}10}$) and soil bulk density (BD) were performed by extracting undisturbed soil cores in 250 cm^{-3} cylinders (Baize 1988) between 0-10 cm. Soil samples at 20-30 cm were collected to obtain $SW_{20\text{-}30}$. All soil samples were stored in closed plastic bags and weighed in the field.

Soil samples for root biomass were collected at 0-10 cm depth on the same plot with cylinder 10 cm length and 15 cm diameter. Soil samples for the measurement of root biomass were sieved at 2 mm and washed with clean water to separate roots and soil. Roots were dried at 70 ºC for 48 h and weighed.

2.3 Laboratory analyses

2.3.1 Vegetation and grass leaf analyses

All grass and non-grass biomass samples from the 50*50 cm plots were dried at 70 ºC for 48 h, and then weighed. Grass green leaves of April 2009 were milled at 1 mm prior to chemical analysis at the University of KwaZulu-Natal. Total grass leaf nitrogen (N_{grass}) was analyzed with a Leco FP2000 Nitrogen Analyzer using the Dumas combustion method from AOAC Official Method 990.03 (Kenneth, 1990). Phosphorus (P_{grass}) was analyzed by digestion with sulphuric acid, hydrogen peroxide and a selenium catalyst using a block digester at 360 °C, and then using a Technicon autoanalyzer II that measures the absorbance of the phosphomolybdovanate complex at a wavelength of 420 nm. The N_{grass}:P_{grass} ratio was then calculated to test for nutrient limitation (Koerselman and Meuleman 1996). Grass fiber content was analyzed to evaluate grass quality since the higher the fiber, the harder herbivore assimilation. The acid detergent fibre (ADF) content was assessed with a Dosi-Fibre machine according to the AOAC Official Method 973.18 (Kenneth, 1990) and the neutral detergent fiber (NDF) was assessed with the same machine but with the method described by Van Soest et al. (1991). Gross energy (GE) contained in grass was measured using a digital data system isothermal CP500 bomb calorimeter. Dry matter digestibility was measured *in vitro* with cellulose enzymes as described by Zacharias (1986).

2.3.2 Soil analyses

SW and BD samples were oven dried at 105 °C for 24 h and weighed. Soil samples from 0-20 cm were air-dried and sieved through a 2 mm grid. Total soil nitrogen (N_{soil}) and total soil carbon (C_{soil}) were analyzed by automated Dumas dry combustion method using a LECO CNS 2000 (Matejovic, 1996). Soil pH was determined in 1:2.5 soil:water suspensions. Cation exchange capacity (CEC) was assessed with the Metson method (Metson, 1956); the exchangeable cations Ca^{2+}, Mg^{2+}, K^{+}, Na^{+} and their sum were quantified with the ammonium acetate method at pH 7.0.

2.4 Statistical analyses

Response variables were grouped in three categories.

- Description of the herbaceous community: dry grass biomass, dry non-grassy biomass, grass green leaf biomass, grass species richness, non-grass species richness.
- Grass quality: dry matter digestibility, N_{grass}, P_{grass}, N_{grass}:P_{grass} ratio, GE, ADF, NDF.
- Soil properties: SW at 0-10 cm, SW at 20-30 cm, BD, total C_{soil}, total N_{soil}, pH, exchangeable Na^{+}, Ca^{2+}, Mg^{2+}, K^{+}, CEC.

Different statistical models were applied in this study as explained below using R version 2.11.1. free online software (http://www.R-project.org).

To test *Season* effect on variables measured in both periods, we used a mixed generalized linear (GLIM) model to take into account the temporal pseudo-replication from sampling the same individuals (tall acacias, medium-sized acacias or control) in two different periods. Fixed factors were *Season*, (Dry, Wet), *Tree* (Tall acacias, Medium acacias, Controls), *Position* in the catena (Upper, Middle, Lower), *Livestock* (Fenced, Unfenced) and the plot was considered as a random factor. Because *Season* affected almost all variables, to aid interpretation of the other factors, we also analyzed each sampling period separately. To test for the effect of *Tree*, *Position* and *Livestock* on each response variable described above for each season, we used a three-way ANOVA with *Tree*, *Position* and *Livestock* as factors. Normality of residuals and homogeneity of variance were tested for each model. Variables with non-normally distributed residuals or non-homogeneous variance were log-transformed or square root transformed.

The presence/absence of the main grass and non-grass species were analyzed separately by three-way factorial analyses of deviance (using a binomial model due to the binary format of the variables) with *Tree*, *Position* and *Livestock* as factors. Dominance of each grass species on a plot (where the concerned grass species was the most abundant) was tested following the same method. Even if dry biomass was measured for each non-grassy species, the high frequency of zeroes did not allow us to apply a generalized linear model to these data (none of the possible transformations was adequate and model residuals were not normal). We thus transformed the data into binary format to analyze their deviance as described above. We tested the presence/absence and then the number of plots where non-grassy biomass was greater than the third (upper) quartile.

Because of the high number of statistical tests in this study, and to avoid rejecting a null hypothesis when it is actually true (type I error) we applied adjusted Bonferroni corrections to p values for each group of variables (vegetation quantity, grass quality and soil properties) for all analyses. Similarly, *post hoc* t-tests with Bonferroni corrections were always used to compare means between the significant factors.

Table 1. Four-way ANOVA results (F values) of simplified mixed model for variables of both seasons with fixed factors *Season* (Dry, Wet), *Tree* (Tall, Medium, Control=no acacia), *Position* in catchment (Upper, Middle, Lower), *Livestock* (Fenced, Unfenced) and with a random term for each plot. Three-factor and four-factor interactions were not significant and are thus omitted. Adjusted Bonferroni corrections were applied to p values. * indicates significant p values. Each model was simplified so some F values are not displayed (-).

Vegetation variables	Error d.f.	Season	Tree	Livestock	Tree: Livestock	Season: Position	Season: Tree
Root biomass	64	-	3.23*	0.35	3.64*	-	-
Dry grass biomass	60	124.85*	5.05*	9.26*	-	-	-
Non-grass biomass	61	23.33*	-	-	-	2.86*	-
Non-grass species richness	63	28.84*	10.09*	0.99	2.85	-	-
Soil variables					Position		
Soil Moisture $SW_{0\text{-}10\ cm}$	61	1378.27*	-	-	33.11*	3.50	5.45*
Soil Moisture $SW_{20\text{-}30\ cm}$	61	1797.83*	-	-	15.91*	3.12	4.88*
BD	58	107.37*	3.88*	11.91*	4.90*	-	-
Total C (C_{soil})	63	21.55*	-	-	16.65*	-	-
Total N (N_{soil})	61	1.252	5.36*	1.44	9.943*	-	15.63*

3. Results

3.1 Complete model for both seasons

Season had an important effect on vegetation and soil variables. Root biomass was the only one of nine variables measured in both periods that did not show any significant *Season* effect (Table 1). The only significant effect implicating *Season* on total soil nitrogen was the interaction *Season*X*Tree* (Table 1).

We present here a short description of the variables significantly affected by *Season* as they will be presented in details for other factors for each season in the next section:

Soil variables

SW_{0-10} and SW_{20-30} respectively increased by 14.9 % and 10.8 % in April. C_{soil} and BD were lower in April (C_{soil}: 17.5 ±2.7 g kg^{-1}, BD: 1.29 ±0.07 g cm^{-3}) than in November (C_{soil}: 18.95 ±3.2 g kg^{-1}, BD: 1.39 ±0.04 g cm^{-3}).

Herbaceous community

Dry grass biomass was much higher in April (453 ±211 g m^{-2}) than in November (222 ±143 g m^{-2}). Non-grass biomass and non-grass species richness followed the same pattern: *viz*. 35.8 ±24.5 g m^{-2} and 5.59 ±1.95 species per plot in April and 21.6 ±22.4 g m^{-2} and 3.81 ±2.64 species per plot in November. In November 2008, a high biomass of *Senecio inaequidens* was harvested (22.68 ± 32.52 g m^{-2} on average). This biomass was almost 10 times higher than the biomass harvested in April 2009 (2.4 ±7.1 g m^{-2} on average). Due to the seasonal cycles of *Senecio inaequidens* and a late start to the wet season, November 2008 samples were old, dry shoots of the previous growing season (2007-2008), while April 2009 samples were new green shoots from the recent growing season (2008-2009).

Variables not affected by season are presented here in details. Root biomass showed a significant *Tree* effect and *Tree*X*Livestock* interaction (Table 1) for both seasons. For unfenced plots, root biomass was lower under tall acacias than in control plots with 7.96 ±3.04 g l^{-1} and 12.17 ±4.59 g l^{-1} respectively (Fig. 1A).

There was a significant difference in N_{soil} between November and April only under tall acacias (Fig. 1B) with 1.8 ±0.24 g kg^{-1} and 1.6 ±0.26 g kg^{-1} respectively.

Moreover, N_{soil} had higher values under tall acacias than medium acacias and control plots in the dry season. N_{soil} increased by 17.4 % under tall acacias compared to medium acacias and by 15.76 % compared to control plots (Fig. 1B). N_{soil} was also higher in the middle part of the watershed for both seasons with 1.7 ±0.24 g kg^{-1} versus 1.6 ±0.23 g kg^{-1} in lower part and 1.5 ±0.23 g kg^{-1} in the upper part (Fig. 1C).

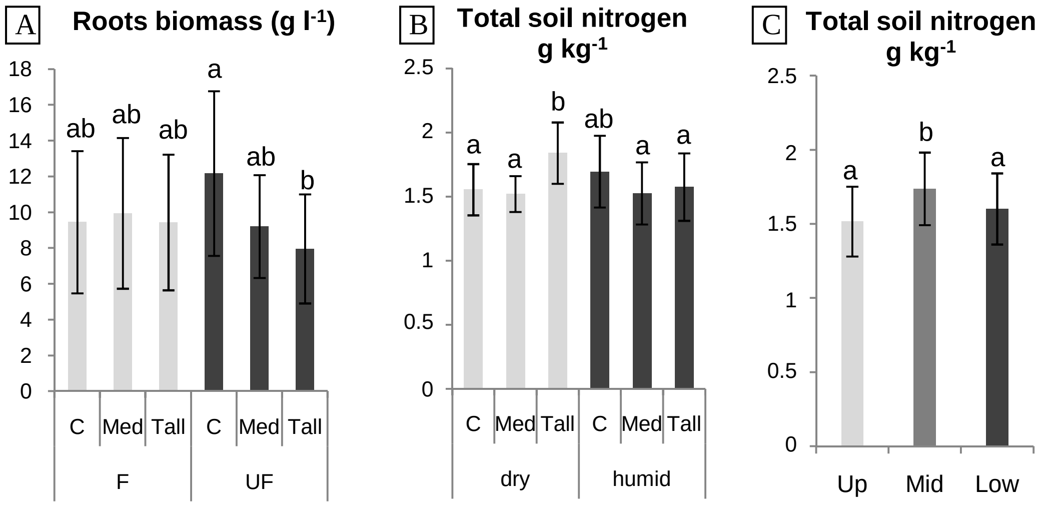


Figure 1. Effect of *Tree*, *Livestock* and *Position* for response variables which do not show significant results for *Season* effect. Means and standard deviation are displayed. Different letters indicate significant differences between means. *F*: fenced, *UF*: unfenced; *dry*: dry season, *wet*: wet season; *C*: control, *Med*: medium acacia, *Tall*: tall acacia. *Lower*, *Middle*, *Upper* refer to the position in the landscape.

Table 2. Three-way ANOVA results (F values) in **April 2009** for vegetation variables with *Tree* (Tall, Medium, Control= no acacia), *Livestock* (Fenced, Unfenced) and *Position* in catena (Upper, Middle, Lower). Only the interaction *TreeXLivestock* showed significant results and is thus presented here. Gross energy was analyzed by a generalized linear model. Three-factor and four-factor interactions were not significant and are thus omitted. Analyses as for Table 1.

Grass quantity variables	Error d.f.	Tree	Livestock	Position	Tree: Livestock
Dry grass biomass	62	-	76.66*	-	-
Grass green leaf biomass	58	1.96	2.07	-	5.45*
Grass species richness	62	-	4.64*	-	-
Non-grass species richness	61	6.10*	-	-	-
Grass leaf quality variables					
Digestibility	60	4.64*	24.15*	-	-
Nitrogen (N_{grass})	58	30.23*	34.40*	-	5.99*
Phosphorus (P_{grass})	56	0.15	22.90*	4.58*	3.65*
N_{grass}:P_{grass}	59	7.89*	-	4.76*	-
Gross energy	63	4.21*	-	-	-
ADF	62	-	45.79*	-	-
NDF	58	-	-	-	5.17*

3.2 April 2009 (end of wet season): *Tree, Livestock* and *Position* effect

3.2.1 Vegetation variables

The *Position* in the watershed had no effects on *vegetation* variables except for P_{grass} and N_{grass}:P_{grass} ratio (Table 2). P_{grass} was significantly affected by *Position,* with higher values in the middle (8.2 ±1.6 %) than in the lower part (6.8 ±1.5 %) of the catena. Contrastingly, the N_{grass}:P_{grass} ratio had lower values in the middle (16.1 ±2.7) than in the lower part (18.9 ±3.6) of the catena.

Livestock and *Tree* affected a number of vegetation variables: dry grass biomass was affected by *Livestock* and was higher in fenced plots than unfenced plots (Fig. 2a). This effect was similar for grass species richness and ADF (Fig. 2b and 2c). However, digestibility, N_{grass}, and P_{grass} had significantly higher values in unfenced plots (Fig. 2d, 2e, 2f).

Tree had a significant effect on non-grass species richness: the number of non-grass species was higher under medium acacias than on control plots (Fig. 2g). Digestibility was also affected by *Tree* with higher values under tall acacias than medium acacias (Fig. 2h). N_{grass} was significantly higher under tall acacias and medium acacias than on control plots (Fig. 2e). The N_{grass}:P_{grass} ratio had significantly lower values for controls than medium and tall acacias whereas GE had lower values for medium acacias than controls and tall acacias (Fig. 2i and 2j). NDF was only significantly affected by *Tree*X*Livestock* interaction, with controls having higher NDF values than medium acacias for fenced plots (Fig. 2k). Similarly, grass green leaf biomass was significantly affected by *Tree*X*Livestock* interaction; it was higher under tall acacias than on control plots for the unfenced treatment (Fig. 2l).

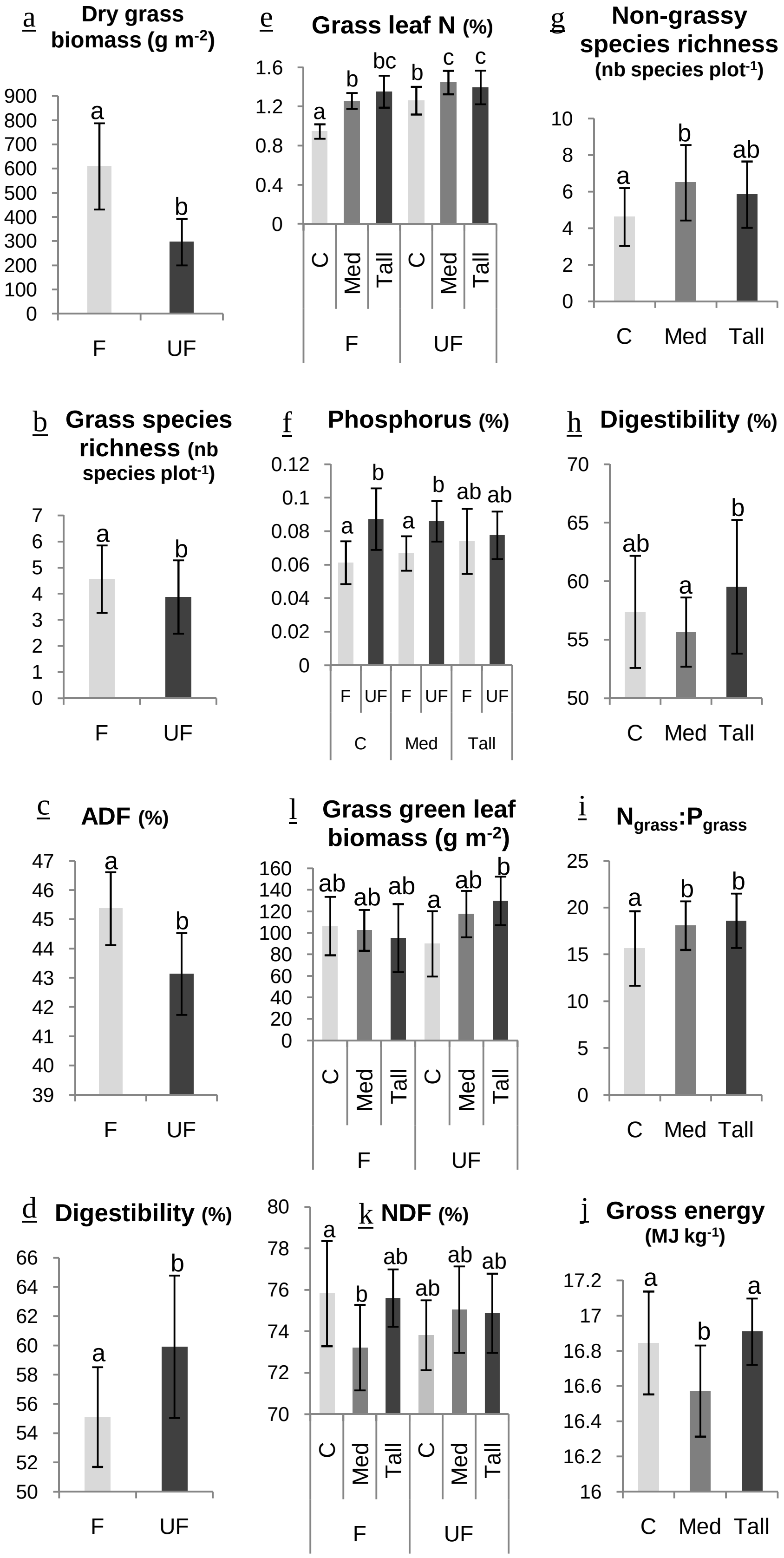


Figure 2. Effect of main significant results of explanatory variables on **vegetation variables in April 2009**. Means and standard deviation are displayed. Letters indicate significant p values between treatments. *F*: Fenced; *UF*: Unfenced; *C*: control; *Med*: medium acacia; *Tall*: tall acacia.

Grass and non-grassy species

Hyparrhenia hirta and *Sporobolus africanus* (Poir.) Robyns & Tournay were the two main grass species found in this grassland. They were present on 50 and 48 plots respectively of a total of 64 plots. They were also the most *abundant* species on 30 and 20 plots respectively (Table 3) and the second most abundant on 15 and 21 plots respectively.

Table 3. Three way factorial analyses of deviance (deviance values) on the 7 most frequently-observed grass species with *Tree* (Tall, Medium, Control=no acacia), *Position* in catena (Upper, Middle, Lower) and *Livestock* (Fenced, Unfenced). *Tree* was not significant and is thus omitted. Interactions are indicated with light grey color. NP is the number of plots where the species and dominant species were observed from a total of 64 plots. Absence of value (-) means that it has not been included into the analyses due to very low occurrence (*cf* NP). Analyses as for Table 1.

	Presence/Absence			1st dominant	
Grass species	NP	Livestock	Position	NP	Livestock
Hyparrhenia hirta	50	8.4*		30	6.48*
Sporobolus africanus	48	20.1***	ns	20	37.15***
Digitaria longiflora	30	ns	16.45**	1	-
		9.37*			
Paspalum scrobitulatum	25	8.27*		0	-
Eragrostis plana	23	5.78*		5	-
Eragrostis curvula	18	ns	9.77*	5	-
Themeda triandra	14	6.95*	ns	3	-

Tree had no significant effect on grass species whereas *Livestock* and *Position* affected grass species significantly (Table 3). *Hyparrhenia hirta* was more frequently present in the lower part of the catena (all plots) than in the upper part (only on 54.5 % of the plots). This result was especially clear when livestock were present. *Paspalum scrobitulatum* (L.) showed similar results, with a higher presence in the lower part (58.3 % of the plots against 10 % in upper part) but only when livestock were absent. Conversely, *Digitaria longiflora* (Retz.) Pers. and *Eragrostis curvula* (Schrad.) Nees were more frequently present in the upper part than in the middle and lower parts of the catena (Table 3). The presence of *Eragrostis plana* (Nees) and *Themeda triandra* was affected by livestock with a higher presence in fenced (50 % and 34 % of the plots, respectively) than unfenced plots (21 % and 12 % of the plots, respectively). *Sporobolus africanus* showed the opposite pattern, being present in 97 % of the unfenced plots and 53 % in the fenced plots (Table 3). For the two most common species, we investigated the number of plots where the species were dominant (the most abundant among all grass species present on the plot). *Hyparrhenia hirta* was twice as dominant in fenced (62 %) than unfenced plots (31 %) whereas *Sporobolus africanus* was the most abundant in 62 % of the unfenced plots and was never dominant in fenced plots (Table 3).

Unlike grass species, non-grass species were affected by *Tree* and by *Livestock* (Table 4). The dominant invasive species *Richardia braziliensis* (Moq.) was present in all plots but its highest biomass was mainly in control plots (25 % of the plots). *Sida dregei* Burtt Davey was more common under tall acacias for 50 % of the plots and only 8.3 % of the control plots and 10% of the medium-sized acacia plots. *S. dregei*'s highest biomass was under tall acacias (35 % of the plots). *Senecio inaequidens* are only found under acacia (25 % of tall acacia plots and 35 % of medium acacia plots). *Hibiscus pedunculatus* L.f. was only present under tall acacias in 20 % of the plots. *Centella asiatica* (L.) Urban was the only species significantly affected by *Livestock* and was present in 28.1 % of fenced plots vs 6.25 % of unfenced plots (Table 4).

Table 4. Three way factorial analyses of deviance (deviance values) on the 7 most frequently observed non-grassy species with *Tree* (Tall, Medium, Control=no acacia), *Position* in catena (Upper, Middle, Lower) and *Livestock* (Fenced, Unfenced). *Position* and all interactions were not significant and are thus omitted. Analyses as for Table 1.

		Presence/Absence	Highest Biomass	
Non-grassy species	Total biomass harvested	Tree	Tree	Livestock
Richardia braziliensis	179.85	ns	9.25*	ns
Sida dregei	68.35	12.74*	18.28***	ns
Vernonia natalensis	38.34	ns	ns	ns
Senecio inaequidens	35.98	13.37**	7.26*	ns
Centella asiatica	17.4	ns	ns	5.74*
Hibiscus pedunculatus	12.02	9.9*	ns	ns

3.2.2 Soil variables

Na^+ and K^+ ions were not affected by any of the factors tested in this study and are thus not presented in Table 5. Other soil variables were affected mainly by *Tree* and *Position* (Table 5). *Livestock* effect was only significant for BD and pH (data not shown graphically). *Livestock* increased values of BD and pH in unfenced plots (bulk density, unfenced 1.33 ±0.06 g cm^{-3}, fenced 1.27 ±0.06 g cm^{-3}; pH, unfenced 5.99 ±0.15, fenced 5.90 ±0.16).

Tree had a significant effect on all variables except for SW and pH. CEC, Ca^{2+}, Mg^{2+} followed the same pattern with lower values in controls and under medium acacias than under tall acacias (Fig. 3a). C_{soil} was affected by the interaction *Tree*X*Livestock* (Table 5). In unfenced plots, C_{soil} was higher under tall acacias than controls and *vice versa* in fenced plots (Fig. 3b).

The *Position* in the watershed had a strong effect for all soil variables, except Na^+ and K^+. The SW_{0-10} and SW_{20-30} were lower in the upper part of the watershed (Fig. 3c) compared to the middle and lower parts. C_{soil} showed similar results (Fig. 3d). Contrastingly, BD was higher in the upper part than in the middle part of the catena (Fig. 3e). The CEC, as well as Ca^{2+} and Mg^{2+}, had lower values in the lower part of the catena than in the middle and upper parts (Fig. 3f). pH increased significantly from the lower part to the upper part of the catena (Fig. 3g).

Table 5 Three-way ANOVA results (F values) in April 2009 for soil variables with *Tree* (Tall, Medium, no acacias), *Livestock* (Fenced, Unfenced) and *Position* in catena (Upper, Middle, Lower). No interactions were significant and are thus omitted. Analyses as for Table1.

Soil variables	Error d.f.	Tree	Livestock	Position
BD	58	3.44	15.58*	5.26*
Soil moisture SW_{0-10}	61	-	-	24.52*
Soil moisture SW_{20-30}	61	-	-	14.48*
pH	58	-	5.67*	7.56*
Ca^{2+}	59	7.37*	-	13.38*
Mg^{2+}	59	11.49*	-	21.19*
CEC	59	9.22*	-	10.71*
Total C (C_{soil})	56	3.7*		4.94*

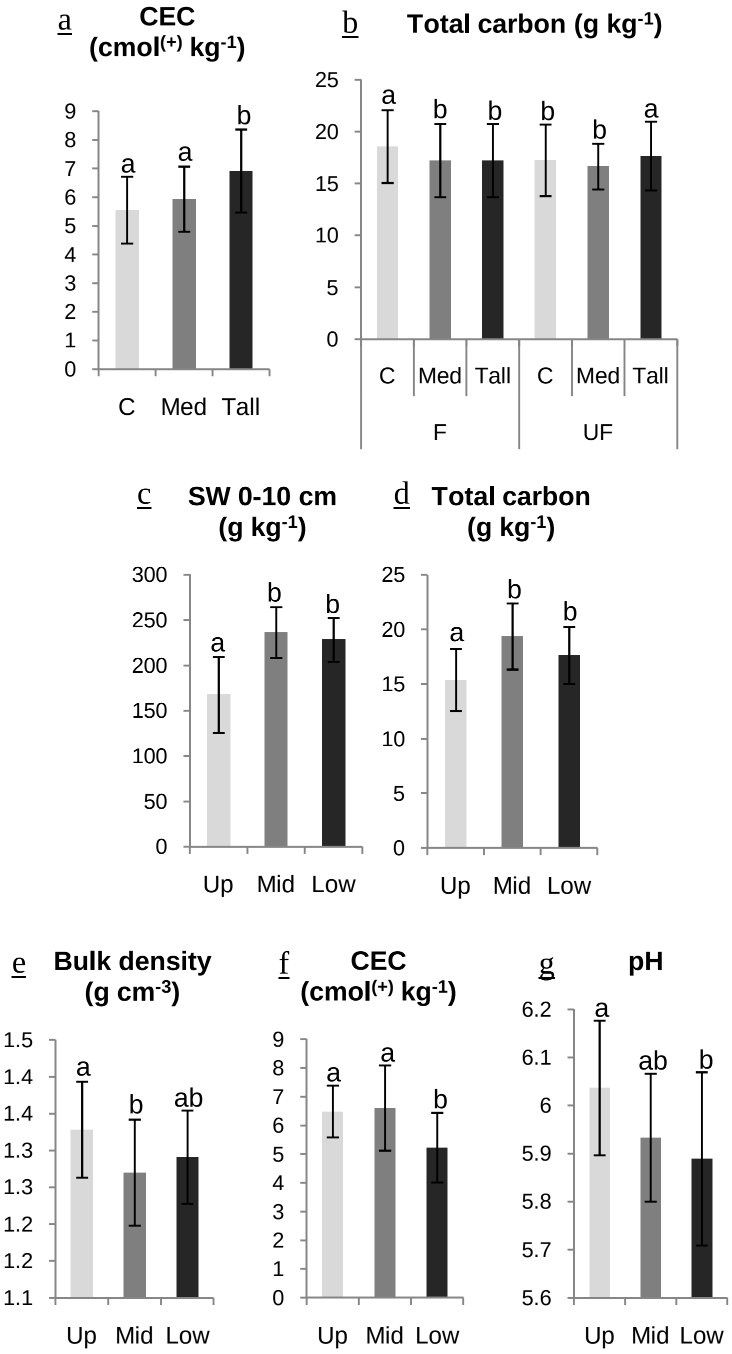


Figure 3. Effect of main significant results of explanatory variables on **soil variables in April 2009**. Means and standard deviation are displayed. Letters indicate significant p values between treatments. *F*: Fenced; *UF*: Unfenced; *C*: control; *Med*: medium acacia; *Tall*: tall acacia; *Low* for lower part, *Mid* for middle part, *Up* for upper part refer to position in catena.

3.3 November 2008 (end of dry season-beginning of wet season): *Tree* and *Position* effect

Tree significantly affected most variables while *Position* only affected soil variables (Table 6). Bulk density did not show any significant pattern (p= 0.58 for *Position*, p= 0.85 for *Fence*, p= 0.13 for *Tree*). *Position* affected SW at both depths in the same way, viz. higher values in middle part of the catena than in the lower and upper parts (Fig. 4A). C_{soil} followed the same pattern (Fig. 4B).

Dry grass biomass showed higher values under medium acacias than controls and tall acacias (Fig. 4C). Non-grass species richness was lower in controls than under medium and tall acacias (Fig. 4D). SW at both depths followed this pattern as well with lower values for controls (Fig. 4E).

Table 6. Three-way ANOVA results (F values) in November 2008 with *Tree* (Tall, Medium, no acacias), *Position* in catchment (Upper, Middle, Lower) and *Livestock* (Fenced, Unfenced). *Livestock* and all interactions were not significant and are thus omitted. Analyses as for Table 1.

Vegetation variables	Error d.f.	Tree	Position
Dry grass biomass	61	3.63*	-
Non-grass species richness	61	8.04*	-
Soil variables			
Soil Moisture SW_{0-10}	41	12.05*	18.34*
Soil Moisture SW_{20-30}	41	8.53*	8.90*
Total C (C_{soil})	61	-	13.53*

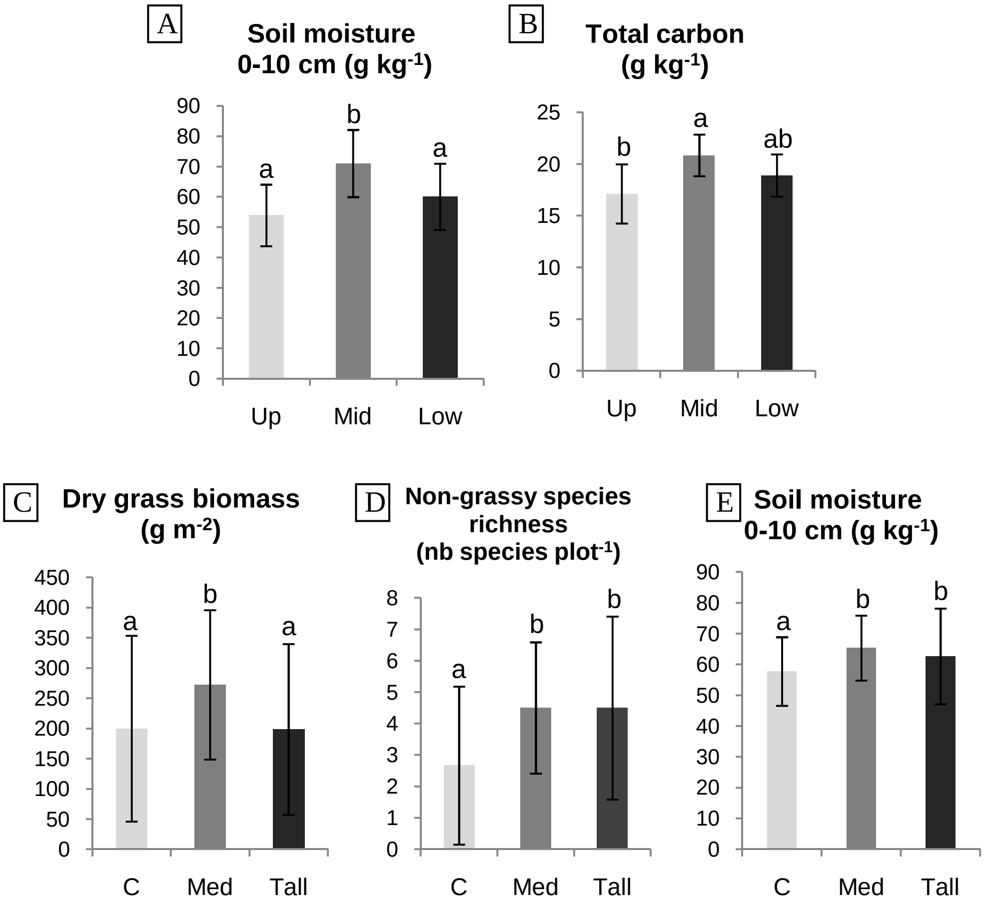


Figure 4. Effect of main significant results of explanatory variables on **variables in November 2008**. Means and standard deviation are displayed. Letters indicate significant p values between treatments. *F*: fenced, *UF*: unfenced; *dry*: dry season, *wet*: wet season; *C*: control, *Med*: medium acacia, *Tall*: tall acacia. *Up, Mid*, *Low*, refer to the position in the landscape.

4. Discussion

4.1 Do trees have an impact on grass and soil properties?

This question can be answered from the most complete data set of April. This study showed that acacias did not have an important impact on soil properties in wet season. C and N have been reported to accumulate in the soil following woody plant invasion (Wiegand et al., 2005; Liao et al., 2006) and total soil N is often higher under trees than in the open grassland (Abule et al., 2005) especially with leguminous trees (Wiegand et al., 2005; Treydte et al., 2007) due to their N-fixation capacity. However we did not observe such impacts in April, which may be linked to the increase of N_{grass} in grass leaf under acacias. N_{soil} may have been exported into grass leaves during the grass growth period.

Mg^{2+} and Ca^{2+} increased under acacias, as has been found elsewhere in South Africa (Trinogga, 2010). This can be explained by litter input into the soil and by the base-pump function of trees and shrubs which reallocate nutrients from lower soil layers to the surface. Exchangeable cations are usually associated with pH increase (Hatton and Smart, 1984), which was not the case in this study. Exchangeable cations and pH are linked by the capacity of the soil to store charges, which is recorded as CEC. In this study, CEC was found to be higher under acacias, as was also found by Trinogga (2010). This increase was likely due to litter input and decomposition which allows increases in Mg^{2+} and Ca^{2+} without a decrease in H_3O^+ (or an increase in pH).

Dry grass biomass in April 2009 did not differ below tall or medium acacias and controls, as was also found by Abule et al. (2005), Treydte et al. (2007), and Ludwig et al. (2004; 2008). Only a few studies in South Africa and central USA have reported negative effects of trees on grass productivity (Hoffman and Ashwell, 2001; Lett and Knapp, 2003) mainly due to competition for light and nutrients. N_{soil} content, which was similar under acacias and control plots does not promote grass growth under acacias and is consistent with our dry grass biomass results.

Although acacias did not modify grass biomass in our study, they increased non-grass species richness in April, especially under medium-sized acacias. Ruthven (2001) found similar results. Other authors related grass species richness to pH: lower pH increased species richness due to its effect on the availability of certain nutrients (Fynn et al., 2005; Tisdale et al., 1993). In our case, soil pH cannot explain the increase of non-grass species richness because it was not lower under acacias. Lower temperatures and evapotranspiration often measured under trees (Belsky, 1994) have been shown to modify the presence/absence of grass species, depending on their water-use efficiency (Amundson et al., 1995). This could also be the case for non-grass species. The increase in non-grass species richness under acacias was also the sign of a difference in species composition between acacia canopy and open grassland. *Sida dregei, Senecio inaequidens* and *Hibiscus pedunculatus* were found mainly under acacias. *Senecio inaequidens,* due to its toxicity (Dimande et al., 2007) for cattle and horses (Botha and Penrith, 2008) through the presence of pyrrolizidine alkaloids, could have a major negative impact on horses and cattle grazing in the grassland. *S. inaequidens* grows more frequently and gets larger under *A. sieberiana* (tall and medium trees) in this grassland and is likely to create areas that cattle avoid. The available grazing area is thus likely to decrease because of the presence of *S. inaequidens*. This was confirmed by our observations in the field and has been reported by local herdsmen.

'Islands of fertility' is a well-known expression to describe isolated trees or tree clumps in grassland and savanna (Hibbard et al., 2001; Ludwig et al., 2008; Van Auken, 2009), especially when leguminous trees are involved (Treydte et al., 2007; Wiegand et al., 2005). It has often been found that nutrient and protein content, gross energy and digestibility of grass leaves are higher and fibre content lower under trees than in the open grassland (Ludwig et al., 2008). In our study, N_{grass} as well as N_{grass}:P_{grass} ratio followed this tendency, i.e. being higher under acacias than in the open grassland. Higher availability of N_{soil} may increase N_{grass}. With values over 15 (Koerselman and Meuleman, 1996) or 12 (Ludwig et al., 2001) for tropical grassland, N_{grass}:P_{grass} ratio indicates that P_{soil} was the limiting factor to grass growth (Cech et al., 2008).

4.2 Is the size of trees important?

Other grass traits did not show the same pattern, at least under medium-sized acacias. Medium acacias had a negative impact on grass gross energy and digestibility whereas controls and tall acacias did not differ in grass leaf digestibility, gross energy and NDF. All the benefits brought by tall acacias due to their shade (Belsky, 1994), root nodules (Belsky et al., 1989), hydraulic lift capacity (Ludwig et al., 2001), and litter fall (Hudak et al., 2003) are probably counteracted by competition for water and nutrients (Ludwig et al., 2004) and result in an almost neutral effect of these large acacias on grass quality. Medium-sized acacias, with fewer positive benefits due to their size (for the above-mentioned reasons) may compete with grass and resulted in a net negative effect on grass quality.

4.3 Does the impact of trees on grass and soil layers change with the season?

The interaction *Season*X*Tree* indicated that *Season* had a significant effect on the impact of acacias on soil variables but not on plant biomass (Table 1). $SW_{0\text{-}10}$ and $SW_{20\text{-}30}$ were higher below acacias when water was scarce in November, but this effect disappeared during the wet season. This pattern could be related to hydraulic lift as described in some African savannas (Ludwig et al., 2003): trees favor uplift water from deep moist soil layers and release some of this water in superficial dryer soil layers at night, especially when the difference in moisture between depth and surface is high. This pattern could also be due to the shading of acacia canopy that is likely to decrease temperature and evapotranspiration (Belsky 1994). This effect might maintain higher moisture content under acacias at the beginning and at the end of the wet season, thereby extending growth period of grasses.

Season had a significant effect on N_{soil}. In November 2008, we observed that tall acacias show higher N_{soil} contents than medium acacias and controls. This effect was not observed in April 2009 as mentioned above. The explanation may come from two processes: either N produced by nodules decreases in April or N_{soil} is exported to other compartments. The first cause may happen if the availability of N_{soil} increases, which usually reduces nodulation (Cramer et al., 2007). The second cause may be explained by lixiviation of N_{soil} by heavy rainfalls of wet season or linked to N cycle (Aranibar et al., 2004): even if we did not measure other forms of nitrogen in the soil to obtain information on N cycle, N_{grass} under acacias in April was higher than in control plots. This indicates that the possible excess of mineral N_{soil} available under acacias might have been taken up by grasses and stocked into their leaves during their growth period. This explanation relies on a quick mineralization of the increased total N_{soil} detected in November.

In November 2008, higher dry grass biomass was measured below medium acacias, but not tall acacias. This cannot be explained by higher N_{soil} availability as Fynn et al. (2005) suggested because lower N_{soil} content was measured under medium acacias. However, light is more accessible for grasses under medium acacias (due to their lower canopy size) and competition for water may be lower as well compared to taller acacias. This could result in a net positive effect for smaller and less competitive acacias. In April this effect is cancelled because water does not limit grass growth. Indeed, dry grass biomass increased during the wet season. As shown by soil moisture data, the main driving forces explaining differences between both periods is the availability of water and the seasonal cycle, which affects most vegetation variables.

In November 2008, for the first sampling period at the end of the dry season-beginning of the wet season, most grass species had not started growing whereas non-grass species had already begun growth, except *S. inaequidens.* This species differed from the other species because it did not grow equally well in both years, with a biomass 10 times higher in November (composed mainly of dry shoots from the previous growing season S1). Degradation of the grass layer has been shown to be the main factor fostering invasions by *S. inaequidens* (Caño et al., 2007). However, the grass cover in the grassland in the 2007-2008 season (S1) was not obviously more degraded than in the 2008-2009 season (S2) (pers. obs.). Growing season S1 had a slightly higher amount of rainfall than S2 (1010 mm in S1 and 871 mm in S2) which could favor *S. inaequidens* growth. Moreover, rainfall in S2 started very late (at the end of November) after our sampling while it usually starts at the beginning of October. As *S. inaequidens* is a robust species (Caño et al., 2007) it may have started growing in S2 before the grass species. Goats and sheep are known to eat *Senecio* without being affected by its toxicity and may regulate the invasion of this species (Dollahite 1972). They probably fed on *S. inaequidens* at the beginning of S2 (after our first sampling) and drastically decreased the biomass of *S. inaequidens* in the grassland between the two sampling periods.

4.4 How does livestock affect tree-grass interactions?

Livestock affected tree-grass interactions through several variables: C_{soil} which is often higher under trees (Abule et al., 2005; Treydte et al., 2007) followed a similar pattern in our study but only when livestock were present. This suggests that C_{soil} in our site might increase mainly under acacias through dung deposition by cattle (Belsky et al., 1989).

Root biomass was higher in control plots than under tall acacias only when livestock were present. Grass shoot:root ratio can be modified depending on species-specific responses of grasses to grazing (Li et al., 2005). To avoid *S. inaequidens* located mainly under acacias, cattle may graze preferentially outside of the acacias influence. Grazing of aboveground parts of the grass layers, mostly in open grassland, may favor grass root growth to compensate for grass removed by cattle as is the case for certain grass species (Li et al., 2005).

Beside the impact of *Livestock* on tree-grass interactions, *Livestock* also had an impact on grass and soil properties. Soil bulk density was higher in unfenced plots. This result has been reported previously and is due to soil compaction by animal trampling (Kölbl et al., 2010). As has commonly been found (Kölbl et al., 2010; Mbatha and Ward, 2010), livestock presence decreased grass biomass by grazing in our study. Grass species richness also decreased with *Livestock* as pointed out by Stammel et al. (2003). Some authors (Guevara et al., 1996; Abule et al., 2005) did not find negative effects of grazing on grass species richness. Our results are probably due to selective grazing which favors the regrowth of only a few, less palatable species. Indeed, the poorly grazed *Sporobolus africanus* (Van Oudtshoorn, 2004) is exclusively found in unfenced plots whereas the highly palatable *Themeda triandra* is more frequent in fenced plots where it can grow without being grazed by cattle. *Hyparrhenia hirta*, the most abundant species in this grassland, had its highest biomass mainly in fenced plots. This species is known to be moderately appreciated by cattle (Van Oudtshoorn, 2004). However, our results suggest that it is significantly grazed, perhaps due to limited grass availability.

Grass quality was positively affected by *Livestock*. Digestibility, N_{grass} and P_{grass} had higher values in unfenced plots, and ADF had lower values, as found by Mbatha and Ward (2010) during the same period of the year, but in a more arid area. Different levels of leaf nutrients between fenced and unfenced plots may be due to several mechanisms: e.g. herbivores maintain regrowth, which results in higher nutrient concentrations (Frank et al., 1998; Mbatha and Ward, 2010); herbivores speed up nutrient cycling which enhances plant nutrition (increase of nutrient uptake by roots) and increases grass nutrient contents (Chaneton et al., 1996; Frank et al., 1998); in response to grazing and increased light availability, grass photosynthetic rates increase, which may lead to higher protein levels (Mbatha and Ward, 2010).

4.5 Does the position of trees in the landscape modify the impact of trees on grass and soil properties?

Position had very few effects on grass variables and no interaction between *Position* and other factors was found. However *Position* affected all *soil* variables. Contrary to Oztas et al. (2003), bulk density was higher in the upper part of the catena. Oztas et al. (2003) explained their results as being due to higher soil moisture in the footslope position, leading to stronger soil compaction. They indicated that grazing pressure was higher in the footslope position, inducing higher bulk density. In our study, despite higher soil moisture in the middle and lower parts of the catena due to topographic effects, soil compaction was not higher in these parts of the catena. We have no precise data on the grazing behavior of livestock but we know that livestock are present in the lower and middle parts and this did not affect negatively soil bulk density. However, the shallower soils in the upper part of the catena were less structured (higher bulk density, lower total carbon) than deeper soils of the middle and lower parts which might explain the higher bulk density of upper part soils in our study. These less structured soils were also shallower than soils in the middle and lower parts. Shallow soils associated with higher slope may have been associated with stronger sheet erosion (Descroix et al., 2008) which has led to decreased total carbon (Fig. 3d) in the upper part of the catena.

The *Position*X*Tree* interaction was not significant for any of the studied variables. This indicates that position does not modify tree-grass interaction. Treydte et al. (2007) showed that trees more positively affect degraded grasslands than grasslands that function well. Even if the upper part of the catena had soils in poorer condition than the middle and lower parts (shallower, more acid, less organic matter and total carbon, higher bulk density and lower moisture), they were not degraded enough to be modified by the presence of acacias. Other areas in the grassland are considered as badlands due to strong gully erosion (unpublished data). Acacias in these specific areas might have a different impact on grass and soil properties as compared to the less degraded grassland studied here in hillslope catena.

4.6 Implications for grassland management

The results of this study provided new insights into the adaptive grassland management of encroached areas. Association of acacias with toxic species has not been reported yet as far as we know but is very important for grassland managers. Tall acacias did not have negative effects on grass quality and soil properties and should be retained in the grassland, at least initially. The first priority should be to control the population of *S. inaequidens* which is toxic for cattle and horses. Goats and sheep have been used to control

Senecio and shrub invasions in the past (Oates, 1956; Dollahite, 1972). Goats and sheep could be used differently and be completely integrated into the management of the grassland. They are present in this grassland but they need to be led to the concerned areas by herdsmen or with the help of mobile fences and rotational grazing. If needed, a manual cutting of *Senecio inaequidens* could be applied.

The results obtained in this study are valid for a low density of acacias (28 acacias ha^{-1} or 10 % of the watershed area) and may change with acacia encroachment. While a low density of trees was shown to favor sub-canopy herbaceous production, high densities could have a more negative impact on understorey vegetation (Riginos et al., 2009) and thus on livestock production. Treydte et al. (2007) recommended keeping tree density lower than 200 trees ha^{-1}. In a second priority, *A. sieberiana* population would have to be controlled to ensure that the grassland does not become woodland and, consequently, inaccessible to cattle. Because acacia wood is used for fuel by the local human community and acacias are a good source of protein for cattle (pods, present on tall acacias mainly, are preferred by cattle), cutting all trees is probably not the best solution and would be an enormous task (Smit, 2004). We would recommend keeping tall acacias (as medium acacias had negative effects on grass quality) to create shade for cattle and to maintain a source of protein from pods. Spatial heterogeneity at the landscape scale should be considered, such as keeping flat areas free of trees whereas areas less accessible to cattle could be maintained with trees. As Smit (2004) discussed, tree effects on grass and soil properties are highly variable, depending on tree density, location, climate and site specificity. Grassland managers should be aware that actions undertaken to decrease tree density will modify the ecosystem. General advice would thus be to favor small-scale actions, allowing adaptation to local conditions and to the evolution of tree encroachment and its effect on soil properties and grass production.

5. Acknowledgements

We would like to thank the Institute of Research and Development (IRD) and the National Research Foundation (NRF) for its financial support as well as the University of KwaZulu-Natal for its technical support. We also thank the community of Potshini where the work was done and especially Sibonelo Mabaso for his contribution in the field. We finally thank Lucas Janeau for his assistance in the study.

6. References

Abule, E., Smit, G.N., Snyman, H.A., 2005. The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the Middle Awash Valley of Ethiopia. Journal of Arid Environments. 60, 343-358.

Amundson, R.G., Ali, A.R., Belsky, A.J., 1995. Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savanna. Journal of Arid Environments. 29, 139-153.

Aranibar, J., Otter, L., Macko, S., Feral, C.J.W., Epstein, H.E., Dowty, P.R., Eckardt, F., Shugart, H.H., & Swap, R.J. (2004) Nitrogen cycling in the soil–plant system along a precipitation gradient in the Kalahari sands. Global Change Biology, 10, 359-373.

Archer, S., Boutton, T.W., Hibbard, K.A., 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze, E-D., Heimann, M., Harrison, S., Holland. E., Lloyd, J., Prentice, I.C., Schimel, D., (Eds.), Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego, pp 115-138.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E., Harris, A.T., 2004. Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources. 29, 261-299.

Baize, D., 1988. Guide des analyses courantes en pédologie. INRA, Paris.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology. 26, 1005-1024.

Belsky, A.J., Nwonga, S.M., Amundson, R.G., Duxbury, J.M., Ali, A.R., 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low- rainfall savannas. Journal of Applied Ecology. 30, 143-155.

Belsky, A.J., 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology. 75, 922-932.

Bond, W.J., 2008. What limits trees in C_4 grasslands and savannas? Annual Review of Ecology, Evolution and Systematics. 39, 641-659.

Botha, G.A., Wintle, A.G., Vogel, J.C., 1994. Episodic late Quaternary palaeogully erosion in northern KwaZulu-Natal, South Africa. Catena. 23, 327-340.

Botha, C.J., Penrith, M.L., 2008. Poisonous plants of veterinary and human importance in southern Africa. Journal of Ethnopharmacology. 119, 549-558.

Caño, L., Escarré, J., Sans, F.X., 2007. Factors affecting the invasion success of *Senecio inaequidens* and *S. pterophorus* in Mediterranean plant communities. Journal of Vegetation Science. 18, 281-288.

Cech, P.G., Kuster, T., Edwards, P.J., Venterink, H.O., 2008. Effects of herbivory, fire and N_2-fixation on nutrient limitation in a humid savanna. Ecosystems. 11, 991-1004.

Chaneton, E.J., Lemcoff, J.H., Lavado, R.S., 1996. Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. Journal of Applied Ecology. 33, 291-302.

Cramer, M.D., Chimphango, S.B.M., Cauter, A.V., Waldram, M.S., Bond, W.J., 2007. Grass competition induces N_2 fixation in some species of African *Acacia*. Journal of Ecology. 95, 1123–1133.

Descroix, L., González Barrios, J.L., Viramontes, D., Poulenard, J., Anaya, E., Esteves, M., Estrada, J., 2008. Gully and sheet erosion on subtropical mountain slopes: their respective roles and the scale effect. Catena. 72, 325-339.

Dimande, A.F., Botha, C.J., Prozesky, L., Bekker, L., Rösemann, G.M., Labuschagne, L., Retief, E., 2007. The toxicity of *Senecio inaequidens* DC. Journal of the South African Veterinary association. 78, 121-139.

Dollahite, J.W., 1972. The use of sheep and goats to control Senecio poisoning in cattle. Southwest Veterinary. 25, 223-226.

Frank, D.A., McNaughton, S.J., Tracy, B.F., 1998. The ecology of the Earth's grazing ecosystems, Profound functionnal similarities exist between the Serengeti and Yellowstone. BioScience. 48, 513-521.

Fynn, R.W.S., Morris, C.D., Edwards, T.J., 2005. Long-term compositional responses of a South African mesic grassland to burning and mowing. Applied Vegetation Science. 8, 5-12.

Graz, F.P., 2008. The woody weed encroachment puzzle: gathering pieces. Ecohydrology. 1, 340-348.

Grellier, S., Kemp, J., Florsch, N., Janeau, J-L., Ward, D., Barot, S., Podwojewski, P., Lorentz, S., Valentin, C., A 64 year study of gully extension and woody plant encroachment in a subhumid grassland of South Africa. Landscape Ecology. Submitted.

Guevara, J.C., Stasi, C.R., Estevez, O.R., 1996. Effect of cattle grazing on range perennial grasses in the Mendoza plain, Argentina. Journal of Arid Environments. 34, 205–213.

Guy, R.M., Smith, J.M.B., 1995. A land potential classification for KwaZulu-Natal. Rep No N/A/95/12, KwaZulu-Natal Department of Agriculture, Cedara, South Africa.

Hatton, J.C., Smart, N.O.E., 1984. The effect of long-term exclusion of large herbivores on soil nutrient status in Murchison Falls National Park Uganda. African Journal of Ecology. 22, 23-30.

Hibbard, K.A., Archer, S., Schimel, D.S., Valentine, D.W., 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology. 82, 1999-2011.

Hoffman, T., Ashwell, A., 2001. Nature divided: Land degradation in South Africa. University of Cape Town Press, South Africa.

Hudak, A.T., Wessman, C.A., Seastedt, T.R., 2003. Woody overstorey effects on soil carbon and nitrogen pools in a South African savanna. Austral Ecology. 28, 173-181.

Kenneth, H., 1990. Official method of analysis of the association of official analytical chemists, 15th edn. Association of official analytical chemists inc, Arlington, Virginia, USA.

King, G.M., 2002. An explanation of the 1:500 000 general hydrogeological map. Department of Water Affairs and Forestry, Pretoria, South Africa.

Knapp, A.K., Briggs, J.M., Collins, S.L., Archer, S.R., Bret-Harte, M.S., Ewers, B.E., Peters, D.P., Young, D.R., Shaver, G.R., Pendall, E., Cleary, M.B., 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Global Change Biology. 14, 615-623.

Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N:P ratio a new tool to detect the nature of nutrient limitation. Journal of Applied Ecology. 33, 1441-1450.

Kölbl, A., Steffens, M., Wiesmeier, M., Hoffmann, C., Funk, R., Krümmelbein, J., Reszkowska, A., Zhao, Y., Peth, S., Horn, R., Giese, M., Kögel-Knabner, I., 2010. Grazing changes topography-controlled topsoil properties and their interaction on different spatial scales in a semi-arid grassland of Inner Mongolia, P.R. China. Plant Soil. 340, 35-58.

Lett, M.S., Knapp, A.K., 2003. Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. Journal of Vegetation Science. 14, 487-496.

Li, J.H., Li, Z.G., Ren, J.Z., 2005. Effect of grazing intensity on clonal morphological plasticity and biomass allocation patterns of *Artemisia frigida* and *Potentilla acaulis* in the Inner Mongolia steppe. New Zealand Journal of Agriculture Research. 48, 57-61.

Liao, J.D., Boutton, T.W., Jastrow, J.D., 2006. Organic matter turnover in soil physical fractions following woody plant invasion of grassland: evidence from natural ^{13}C and ^{15}N. Soil Biology and Biochemistry. 38, 3197-3210.

Ludwig, F., de Kroon H., Prins, H.H.T., 2008. Impacts of savanna trees on forage quality for a large African herbivore. Oecologia. 155, 487–496.

Ludwig, F., de Kroon H., Berendse, F., Prins, H.H.T., 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecology. 170, 93–105.

Ludwig, F., de Kroon, H., Prins, H.H.T., Berendse, F., 2001. Effects of nutrients and shade on tree-grass interactions in an East African savanna. Journal of Vegetation Science. 12, 579-588.

Matejovic, I., 1996. The application of Dumas method for determination of carbon, nitrogen, and sulphur in plant samples. Rostlinna Vyroba. 42, 313-316.

Mayeux, H.S., Johnson, H.B., Polley, H.W., 1991. Global change and vegetation dynamics. In: James, L.F., Evans, O., Ralphs, M.H. Child, R.D., (Eds.), Noxious Range Weeds. Westview Press, Boulder, CO, pp. 62-74.

Mbatha, K.R., Ward, D., 2010. The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. Journal of Arid Environments. 74, 1294-1301.

Metson, A.J., 1956. Methods of chemical analysis for soil survey samples. Rep No 12, DSIR Soil Bureau Bulletin, New Zealand.

Mucina, L., Rutherford, M.C., 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa.

Oates, A.V., 1956. Goats as a possible weapon in the control of the thorn bush. Rhodesia Agricultural Journal. 53-68.

Oztas, T., Koc, A., Comakli, B., 2003. Changes in vegetation and soil properties along a slope on overgrazed and eroded rangelands. Journal of Arid Environments. 55, 93-100.

Ravi, S., D'Odorico, P., Huxman, T.E., Collins, S.L., 2010. Interactions between soil erosion processes and fires: Implications for the dynamics of fertility islands. Rangeland Ecology and Management. 63, 267-274.

Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S.P.J., Downing, T.E., Dowlatabadi, H., Fernandez, R.J., Herrick, J.E., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F.T., Ayarza, M., Walker, B., 2007. Global desertification: building a science for dryland development. Science. 316, 847-851.

Riginos, C., Grace, J.B., Augustine, D.J., Young, T.P., 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of ecology. 97, 1337-1345.

Ruthven, D.C., 2001. Herbaceous vegetation diversity and abundance beneath honey mesquite (*Prosopis glandulosa*) in the South Texas plains. Texas Journal of Science. 53, 171-186.

Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higging, S.I., Roux, X.L., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J., Zambatis, N., 2005. Determinants of woody cover in African savannas. Nature. 438, 846-849.

Scholes, R.J., Archer, S.R., 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics. 28, 517-544.

Schulze, R.E., 1997. South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria, South Africa.

Smit, G.N., 2004. An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. Journal of Environmental Management. 71, 179-191.

Stammel, B., Kiehl, K., Pfadenhauer, J., 2003. Alternative management on fens: response of vegetation to grazing and mowing. Applied Vegetation Science. 6, 245-254.

Tisdale, S.L., Nelson, W.L., Beaton, J.D., Havlin, J.L., 1993. Soil fertility and fertilizers, 5th edn. Macmillan Publishing Company, New York.

Treydte, A.C., Heitkonig, I.M.A., Prins, H.H.T., Ludwig, F., 2007. Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology, Evolution and Systematics. 8, 197–205.

Trinogga, J., 2010. Arid savanna shrubs affect soil chemistry and vegetation cover. Unpubl MSc thesis, Friedrich Schiller University, Jena, Germany.

Turner, B.L.I., Clark, W.C., Kates, R.W., Richards, J.F., Mathews, J.T., Meyers, W.B. 1990. The Earth as transformed by human action. Cambridge University Press, New York.

Van Auken, O.W., 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management. 90, 2931-2942.

Van Oudtshoorn, F.V., 2004. Guide to grasses of southern Africa. Briza Publications, Pretoria, South Africa.

Van Soest, P.J., Roberston, J.B., Lewis, B.G., 1991. Methods for dietary fibre and nonstarch polysaccharides in relation to animal nutrition. Journal Dairy Science. 74, 3583-3597.

W.R.B., 1998. World reference base for soil resources. Rep N° 84, World Soil Resources Reports, FAO, Rome.

Ward, D., 2005. Do we understand the causes of bush encroachment in African savannas? African Journal of Range & Forage Science. 22, 101-105.

Ward, D., 2010. A resource ratio model of the effects of changes in CO_2 on woody plant invasion. Plant Ecology. 209, 147-152.

Wiegand, K., Ward, D., Saltz, D., 2005. Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. Journal of Vegetation Science. 16, 311-320.

Zacharias, P., 1986. The use of the cellulase digestion procedure for indexing the dry matter digestibility of forages. African Journal of Range & Forage Science. 3, 117-121.

III. Impact des acacias sur les propriétés du sol et de la strate herbacée au sein de ravines d’un pâturage sud-africain

Impact of acacias on grass and soil properties within gullies of an encroached grassland of South Africa

Séraphine Grellier[1]*, David Ward[2], Jean-Louis Janeau[1], Pascal Podwojewski[1], Simon Lorentz[3], Luc Abbadie[4], Christian Valentin[5], Sébastien Barot[6]

[1]IRD-BIOEMCO c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa
[2]School of Biological & Conservation Sciences, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa
[3]School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Box X01 Scottsville 3209, South Africa
[4]CNRS-BIOEMCO, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France
[5]IRD-BIOEMCO, 32 av. H. Varagnat, 93143 Bondy cedex, France
[6]IRD-BIOEMCO, Ecole Normale Supérieure, 46 rue d'Ulm, 75230 Paris 05, France

Keywords: *Acacia sieberiana*, degraded areas, soil protection, livestock

Article in preparation for submission to Journal of Environmental Management.

1. Introduction

The impacts of trees in grasslands have been studied worldwide although inconsistent effects have been reported (Belsky et al. 1993, Treydte et al. 2007, Knapp et al. 2008, Van Auken 2009, Riginos et al. 2009, Grellier et al. submitted). Low fertility savannas tend to show more positive impacts of trees on the grass layer compared to high fertility savannas (Treydte et al. 2007). Some areas of the world are very affected by gully erosion (Valentin et al. 2005), including grasslands. This indicates that tree impacts could differ between eroded areas such as gully areas and the remainder of grasslands. Soil loss by gully erosion is a major problem for grasslands (Podwokewski et al. 2002, Poesen et al. 2003, Valentin et al. 2005). Gully areas usually consist of very poor soil and vegetation cover and can be associated with areas of low fertility. Aboveground vegetation is known to protect soil against erosion through interception of rainfall and better infiltration of water (Podwojewski et al. in press). Roots are also effective protection against erosion by retaining soil (Archibold et al. 2003). Trees may locally favor grass production and enhanced soil properties as suggested by Treydte et al. (2007) for areas of low fertility. In this case, the presence of trees, creating a new ecosystem with a grass layer, may be part of a solution to stabilise gullies.

We conducted a study of the impact of trees on grass and soil properties in gully areas in a grassland of South Africa. This study focuses on acacias which may favor nitrogen input in the soil (Belsky et al. 1989, Wiegand et al. 2005). This input may be important for vegetation growth in the young soils present in gullies similarly to the effects on low soil fertility (Treydte et al. 2007). This study was carried out in two periods of the year to assess the effect of season on the tree-grass-soil system. As livestock may have a strong influence on this grassland ecosystem we also tested the impact of the exclusion of livestock and will examine the following questions:

- Do acacias have a positive impact on grass and soil properties in gullies, especially grass biomass and soil nitrogen?
- How do livestock and season affect tree-grass interactions in gullies?
- Can livestock decrease the potential positive effect of acacias?

2. Materials and methods

2.1 Description of the study site

The description of the study site was done in part II of this chapter.

Regarding the four geomorphological and ecological areas described in part II, we can add a fifth area located at the bottom of the watershed downstream from the fourth area described in part II. This fifth area consists of gully channels where some acacias are established. It is a very heterogeneous area with almost no soil because erosion has often reached the bedrock and because a new soil has often not had enough time to form.

Vegetation is very sparse and is composed of *Aloe ferox*, *Acacia sieberiana*, and few herbaceous species.

2.2 Data collection

2.2.1 Experimental design

In order to understand the impact of the seasons on the tree-grass system, we sampled soils and vegetation during two periods of the year: at the end of the dry season - beginning of the wet season (November 2008) and at the end of the wet season (April 2009). We selected 19 acacias in gullies. Tall acacias that we selected were >3 m height (as were almost all trees in gullies) and located in the most degraded areas of the gullies. We selected 17 locations away from acacias to be used as “controls”, but located on similar substrates as the selected acacias. Fences were erected around three controls and three tall acacias (these numbers were imposed by logistic constraints) in October 2008 to exclude livestock. One extra plot was fenced in February 2008 and retained for this experiment, increasing to four the number of fenced plots for tall acacias. For each plot, one 50 X 50 cm plot was delimited for further soil and vegetation sampling following the same protocol as in the previous part of this chapter.

2.2.2 Laboratory analyses

The same protocol was used as in part II of this chapter.

2.3 Statistical analyses

Response variables were grouped in three categories, as in part II of this chapter.

- Vegetation quantity: dry grass biomass, dry non-grassy biomass, grass green leaf biomass, grass species richness, non-grass species richness.
- Grass quality: digestibility, N_{grass}, P_{grass}, N_{grass}:P_{grass}, gross energy (GE), Acid Detergent Fiber (ADF), Neutral Detergent Fiber (NDF).
- Soil properties: soil moisture at 0-10 cm ($SW_{0\text{-}10}$), soil moisture at 20-30 cm ($SW_{20\text{-}30}$), bulk density (BD), total C_{soil}, total N_{soil}, pH, exchangeable Na^+, Ca^{2+}, Mg^{2+}, K^+, CEC.

Several statistical models were applied in this study (as explained below) using R software (version 2.11.1) (http://www.R-project.org).

We used similar models to those used in part II to test for the *Season* effect (with GLIM) and the effects of *Tree* and *Livestock* for each season separately (two-way ANOVA). Normality of residuals and homogeneity of variance were tested for each model. The analyses of the grass and non-grass species were similar to those in part II, with only two factors: *Tree* and *Livestock*. Because of the high number of statistical tests in this study, and to avoid rejecting a null hypothesis when it is actually true (type I error) we applied adjusted Bonferroni corrections to p values for each group of variables (vegetation quantity, grass quality and soil properties) for all analyses. Similarly, *post hoc* t-tests with Bonferroni corrections were always used to compare means between the significant factors.

3. Results

3.1 Complete model for both seasons

Globally, the results obtained in gullies had very high variability compared to inter-gully areas (see part II of this chapter). *Season* had no significant effect on root biomass (as in the inter-gully area), BD, C_{soil} and N_{soil}. Other variables in both seasons were significantly affected by *Season* (Table 1).

Table 1. Three-way ANOVA results (F values) of the simplified mixed model for variables measured in both seasons with fixed factors *Season* (Dry, Wet), *Tree* (Tall, Control=no acacia), *Livestock* (Fenced, Unfenced) and with a random term for each plot. Adjusted Bonferroni corrections were applied to p values. * indicates significant p values after Bonferroni corrections. Each model was simplified so some F values are not displayed (-).

Vegetation variables	Error d.f.	Season	Tree	Livestock	Tree: Livestock	Season : Tree : Livestock
Dry grass biomass	31	51.89*	7.05*	7.94*	5.55	14.01*
Non-grass biomass	33	12.5*	8.01*	5.87	-	-
Non-grass species richness	33	6.35*	5.71	-	-	-
Soil variables						
Soil moisture SW_{0-10}	33	11.94*	-	-	-	-
Soil moisture SW_{20-30}	33	10.11*	5.95*	-	-	-

All significant variables had higher mean values in April than in November. Dry grass biomass increased from 84.54 ± 98.10 g m^{-2} to 236.52 ± 224.91 g m^{-2} (Fig. 1). Non-grass biomass increased from 9.75 ± 12.98 g m^{-2} to 24.77 ± 28.41 g m^{-2} (Fig. 2A). Non-grass species richness increased from 1.79 ± 1.88 g $plot^{-1}$ to 2.43 ± 2.33 g $plot^{-1}$ (Fig. 2B). Soil moisture SW_{0-10} increased from 130.55 ± 72.74 g kg^{-1} to 164.43 ± 64.31 g kg^{-1} (Fig. 2C) and soil moisture SW_{20-30} increased from 109.41 ± 44.77 g kg^{-1} to 138.93 ± 58.23 g kg^{-1} (Fig. 2D).

Biomass of *Senecio inaequidens* was higher in November 2008 (6.88 ± 18.16 g m^{-2} on average) than in April 2009 (1.55 ± 7.29 g m^{-2} on average) as for the inter-gully areas. Due to the seasonal cycles of *Senecio inaequidens* and a late onset of the wet season, November 2008 samples were old, dry shoots of the previous growing season (2007-2008), while April 2009 samples were new green shoots from the recent growing season (2008-2009).

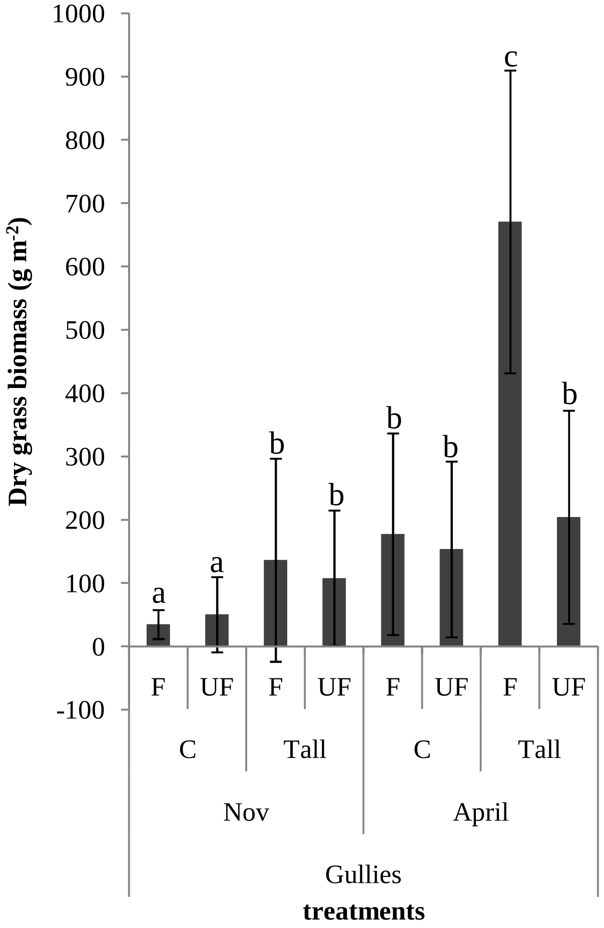


Figure 1. Effects of *Season*, *Tree* and *Livestock* on dry grass biomass. Means and standard deviations are displayed. Letters indicate significant p values between treatments. F: Fenced; UF: Unfenced; C: control; Tall: tall acacia; Nov: November.

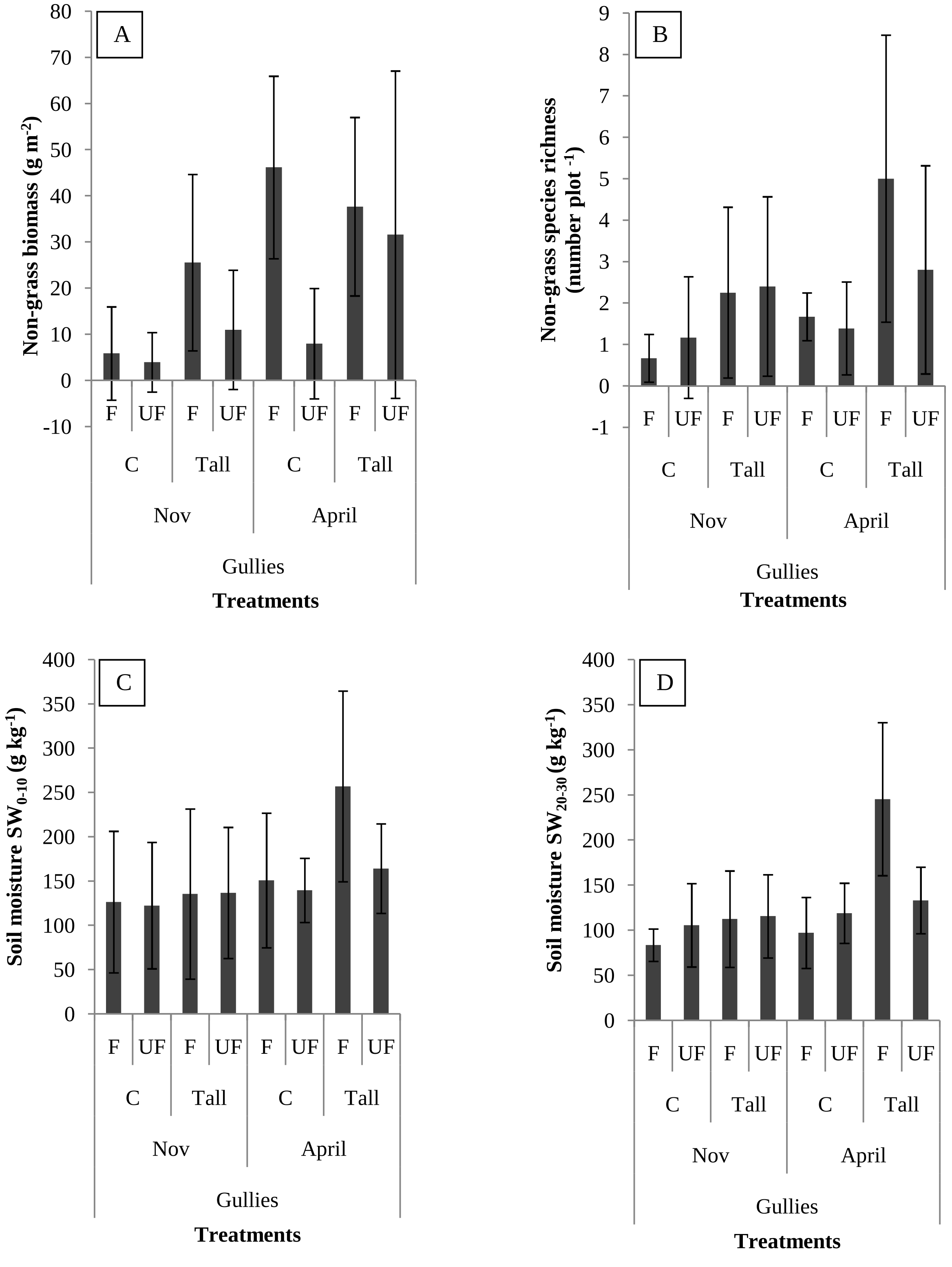


Figure 2. Effects of treatments on non-grass biomass (A), non-grass species richness (B), Soil moisture $SW_{0\text{-}10}$ (C) et $SW_{20\text{-}30}$ (D) in gullies. Means and standard deviations are displayed. *F*: Fenced; *UF*: Unfenced; *C*: control; *Tall*: tall acacia; *Nov*: November.

3.2 April 2009 (end of wet season): *Tree* and *Livestock*

Significant results were hardly reached due to the high heterogeneity of gullies inducing high variability in the results. However, *Tree*, *Livestock* and their interaction had a significant effect on dry grass biomass (Table 2). *Tree* significantly affected GE and Livestock affected grass species richness and non-grass biomass (Table 2).

Table 2. Two-way ANOVA results (F values) in April 2009 for vegetation variables with *Tree* (Tall, Control= no acacia) and *Livestock* (Fenced, Unfenced). Analyses as for Table 1.

Grass quantity variables	Error d.f.	Tree	Livestock	Tree: Livestock
Dry grass biomass	31	6.05*	15.84*	9.82*
Grass species richness	33	-	10.94*	-
Non-grass biomass	28	5.87	11.18*	-
Non-grass species richness	29	5.90	-	-
Grass leaf quality variables				
Gross energy	28	19.57*	5.83	-

Dry grass biomass and GE were higher under acacias than in open areas (Fig. 1 and Fig. 3). Dry grass biomass increased under acacias when they were fenced (Fig. 1, significant interaction *Tree*X*Livestock*). Dry grass biomass (Fig. 1) and GE (Fig. 3) had higher and lower values in fenced plots, respectively. Grass species richness and non-grass species biomass were higher in fenced plots (Fig. 3 and Fig. 2A).

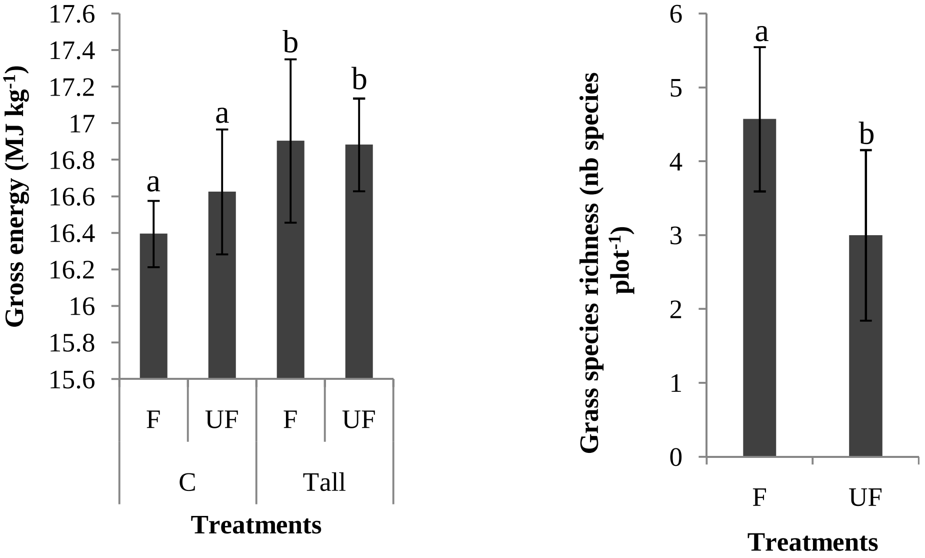


Figure 3. Effects of treatments on gross energy (GE) and grass species richness in April 2009 in gullies. Means and standard deviations are displayed. Letters indicate significant p values between treatments. *F*: Fenced; *UF*: Unfenced; *C*: control; *Tall*: tall acacia.

The main grass species present in the gully were slightly different from those found in the inter-gully area studied in part II (Table 3). Few significant effects were found for the four main species, except for *Eragrostis plana* which were more abundant under tall acacias. Otherwise, *Paspalum scrobitulatum* was only present under acacias and *Cymbopogon plurinodis* was only present on control plots.

Table 3. Two-way factorial analyses of deviance (deviance values) on the 8 most frequently-observed grass species with *Tree* (Tall, Control=no acacia) and *Livestock* (Fenced, Unfenced). The *Tree* X *Livestock* interaction was not significant and is thus omitted. NP is the number of plots where the species and dominant species were observed, from a total of 35 plots. Analyses as for Table 1.

	Presence/Absence			1st dominant		
Grass species	NP	Livestock	Tree	NP	Livestock	Tree
Digitaria longiflora	27	-	-	4	-	-
Sporobolus africanus	17	-	-	5	-	-
Eragrostis plana	15	-	3.95	7	4.28	10.02*
Chloris virgata	11	-	-	3	-	5.03
Hyparrhenia hirta	10	-	-	7	-	-
Paspalum scrobitulatum	6	4.18	8.37*	1	-	-
Sporobolus pyramidalis	6	-	-	3	-	-
Cymbopogon plurinodis	5	-	8.83*	3	4.57	5.03

The non grass species were little affected by *Tree* and *Livestock*. *Schkuhria pinnata* showed higher presence and the highest biomass under acacias (Table 4).

Table 4. Two-way factorial analyses of deviance (deviance values) on the 6 most frequently observed non-grassy species with *Tree* (Tall, Control=no acacia) and *Livestock* (Fenced, Unfenced). *Livestock* and the *Tree* X *Livestock* interaction were not significant and are thus omitted. Analyses as for Table 1.

		Presence/Absence	Highest Biomass
Non-grassy species	Total biomass harvested (g)	Tree	Tree
Sida dregei	72.16	5.13	-
Schkuhria pinnata	37.15	7.86*	10.90*
Senecio inaequidens	13.58	-	-
Ledebouria floribunda	6.43	-	-
Helichrysum rugulosum	5.45	3.9	-
Vernonia natalensis	1.94	-	-

After applying the adjusted Bonferroni correction, only Soil moisture SW_{20-30} was significantly affected by *Tree* and *Livestock* and their interaction (Table 5), presenting higher values under tall acacias and on fenced plots only when associated with tall acacias (Fig. 2).

Table 5. Two-way ANOVA results (F values) in April 2009 for soil variables with *Tree* (Tall, no acacias) and *Livestock* (Fenced, Unfenced). Analyses as for Table 1.

Soil variables	Error d.f.	Tree	Livestock	Tree : Livestock
Soil moisture SW_{0-10}	32	4.6	5.48	-
Soil moisture SW_{20-30}	31	7.28*	11.45*	11.56*
pH	32	7.96	5.58	-
Total N (N_{soil})	33	5.3		-

3.3 November 2008 (end of dry season-beginning of wet season): *Tree* effect

Tree had a significant effect on dry grass biomass (Table 6). Dry grass biomass was higher under tall acacias than in controls with 102.84 ±98.20 g m^{-2} and 39.44 ±35.32 g m^{-2}, respectively. Non-grass species biomass and richness were almost significant and had similar trends as for dry grass biomass. *Livestock* was not tested in November 2008 because fences were erected just prior to the sampling.

Table 6. Two-way ANOVA results (F values) in November 2008 with *Tree* (Tall, no acacias), and *Livestock* (Fenced, Unfenced). *Livestock* and all interactions were not significant and are thus omitted. Analyses as for Table 1.

Grass quantity variables	Error d.f.	Tree
Dry grass biomass	32	5.61*
Non-grass biomass	32	5.31
Non-grass species richness	32	5.38

4. Discussion

4.1 Do trees have a positive impact on grass and soil properties in gully areas?

Acacias did not have an important impact on soil properties in the gullies. Only $SW_{20\text{-}30}$ was higher under acacias in April. In the study of the inter-gully area (*cf.* part II), soil properties were also not very strongly affected by acacias. Only CEC, Mg^{2+} and Ca^{2+} were higher under acacias. This was explained by the input and decomposition of litter under acacias. In the gullies, due to the low vegetation cover (often completely bare soil or bedrock) and the high water flow, acacia leaves are probably easily washed away from under the canopy. The absence of effects of acacias on soil properties, especially N_{soil}, even in such degraded areas, may be linked to the fact that acacias consume all the nitrogen produced by their root nodules. Conditions appear so bad in gullies in terms of nutrients and water availability due to very thin (or even non-existent) soil (Reubens et al. 2009) that acacias did not produce excess nitrogen in the soil.

The main effect of acacias in gullies was on grass biomass, which, unlike in the inter-gully areas, increased significantly under acacias in both seasons. In this degraded area with low vegetation cover and affected by strong evaporation, the acacia shade reduced soil temperature and evapotranspiration (Belsky, 1994), which may be important for the grass layer to develop. Treydte et al. (2007) did not find that grass biomass increased under acacias in low fertility sites. However, they found that grass quality under trees, especially nitrogen and phosphorus content of grass leaves was enhanced in low fertility sites. In our case, gross energy of grass leaves was significantly higher under acacias.

There was a significant impact of acacias on grass species composition unlike in the inter-gully areas. *Eragrostis plana* was more often dominant under acacias. This species is however a poor grazing grass and is usually associated with overgrazing (Tainton et al. 1990). This could be linked to the fact that, in the gullies, cattle grazed more under acacias where grass is more abundant. *Paspalum scrobitulatum* was more common under acacias. It grows in disturbed areas but only when soils are humid enough (Tainton et al. 1990) which may explain their higher frequency under acacias where soil moisture was higher. Contrastingly, *Cympopogon plurinodis* was more common on controls. It is a poor grazing grass due to the essential oils it contains which gives a bitter taste (Tainton et al. 1990). Species such as *Chloris virgata* or *Digitaria longiflora* reflect the poor condition of the gully areas as they are known to grow in disturbed areas (Oudtshoorn 2004).

Non-grass species were little affected by acacias. In contrast to the results presented in part II, there was a non-significant effect of acacias on *Senecio inaequidens*. This result may be due to the much degraded gully areas which do not promote the growth of *S. inaequidens* under acacias or in controls.

4.1 Does the impact of trees on grass and soil properties in gullies change with the season?

The absence of significant interaction between *Tree* and *Season* indicated that the *Tree* effect on grass and soil layers was not modified between the two study periods (Table 1). For both periods, *Tree* significantly affected dry grass biomass. SW_{20-30} was significantly affected by *Tree* in April but not in November, which does not appear as a significant interaction in Table 1. Non-grass biomass was also affected by *Tree* when samples from both seasons were taken into account (Table 1) but not for each season taken separately. This suggests that the number of samples for each season was too low to obtain significant results (Type II error). Despite the higher number of samples taken under acacias and outside of acacia canopies than in the inter-gully area (cf. Part II.), the high heterogeneity of the gullies in terms of soils and vegetation induced high variability. All significant effects of *Season* followed the results obtained for inter-gully areas (cf. Part II). Soil moisture, grass and non-grass biomass and non-grass species increased in April following the vegetation cycle and the higher availability of water in the wet season in April.

4.2 How does livestock affect tree-grass interactions?

Despite the low number of replicates of the *Livestock* treatment, results were significant for some variables. Absence of livestock modified the effects of tree-grass interactions by increasing soil moisture at 20-30 cm and dry grass biomass under acacias in April. *Livestock* effect was thus negative on grass and soil in gullies. These results follow the commonly-reported result that cattle decrease grass biomass by grazing (Kölbl et al. 2010; Mbatha and Ward 2010). As grass biomass was higher under acacias than outside, cattle may have been attracted by the understorey grass when walking in gullies and thus had a greater effect on grass located under acacias than outside. The humidity increase under fenced acacias was thus probably related to the soil protection by the higher grass cover and to the acacia shade which also limits direct evaporation from soil surface.

5. Conclusions

Our results suggest that acacias in gullies may have an important effect on soil stability by increasing grass cover under their canopies. Grasses can modify the hydro-geological processes and the mechanical structure of the soil (Comino and Druetta 2010) and is usually associated with less runoff and erosion (Michaelides et al. 2009, Podwojewski et al. in press). An et al. (2009) suggested that revegetation of eroded soils by grasses accelerates soil rehabilitation. Soil shear strength in gullies was reinforced by grass presence (Dabney et al. 2004). Acacias by itself have also been recognized to limit gully erosion (Reubens et al.

2009). Acacias, associated with protecting gullies from livestock, could help maintaining and even restoring some parts of the gully system and should be kept in the gullies.

6. References

An S.-S., Mentler A., Acosta-Martínez V., Blum W.E.H., (2009) Soil microbial parameters and stability of soil aggregate fractions under different grassland communities on the Loess Plateau, China. Biologia 64:424-427.

Archibold O.W., Lévesque L.M.J., de Boer D.H., Aitken A.E., Delanoy L., (2003) Gully retreat in a semi-urban catchment in Saskatoon, Saskatchewan. Applied Geography 23:261–279.

Belsky A.J., Amundson R.G., Duxbury J.M., Riha S.J., Ali A.R., Mwonga S.M., (1989) The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26:1005-1024.

Belsky A.J., (1994) Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. Ecology 75: 922-932.

Belsky A.J., Nwonga S.M., Amundson R.G., Duxbury J.M., Ali A.R., (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low- rainfall savannas. Journal of Applied Ecology 30:143-155.

Comino E., Druetta A., (2010) The effect of *Poaceae* roots on the shear strength of soils in the Italian alpine environment. Soil and Tillage Research 106:194-201.

Dabney S.M., Shields F.D., Temple D.M., Langendoen E.J., (2004) Erosion processes in gullies modified by establishing grass hedges. Transactions of the ASAE 47:1561-1571.

Grellier S., Ward D., Janeau J.-L., Podwojewski P., Lorentz S., Abbadie L., Valentin C., Barot S., (submitted) Inconsistent environmental impacts of tree encroachment in grassland of South Africa. Journal of Environmental Management.

Knapp A.K., Briggs J.M., Collins S.L., Archer S.R., Bret-Harte M.S., Ewers B.E., Peters D.P., Young D.R., Shaver G.R., Pendall E., Cleary M.B., (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Global Change Biology 14:615-623.

Kölbl A., Steffens M., Wiesmeier M., Hoffmann C., Funk R., Krümmelbein J., Reszkowska A., Zhao Y., Peth S., Horn R., Giese M., Kögel-Knabner I., (2010) Grazing changes topography-controlled topsoil properties and their interaction on different spatial scales in a semi-arid grassland of Inner Mongolia, P.R. China. Plant Soil 340:35-58.

Mbatha K.R., Ward D., (2010) The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. Journal of Arid Environments 74:1294-1301.

Michaelides K., Lister D., Wainwright J., Parsons A.J., (2009) Vegetation controls on small-scale runoff and erosion dynamics in a degrading dryland environment. Hydrological Processes 23:1617-1630.

Oudtshoorn F.V., (2004) Guide to grasses of Southern Africa. Briza Publications, Pretoria, South Africa.

Podwojewski P., Poulenard J., Zambrana T., Hofstede R., (2002) Overgrazing effects on vegetation cover and properties of volcanic ash soil in the paramo of Llangahua and La Esperanza (Tungurahua, Ecuador). Soil Use and Management 18:45-55.

Podwojewski P., Janeau J.L., Grellier S., Valentin C., Lorentz S., Chaplot V., (in Press) Influence of vegetal soil cover on water runoff and soil detachment in a sub-humid South African degraded rangeland. Earth Surface Processes and Landforms.

Poesen J., Nachtergaele J., Verstraeten G., Valentin C., (2003) Gully erosion and environmental change: importance and research needs. Catena 50:91-133.

Reubens B., Poesen J., Nyssen J., Leduc Y., Abraha A.Z., Tewoldeberhan S., Bauer H., Gebrehiwot K., Deckers J., Muys B., (2009) Establishment and management of woody seedlings in gullies in a semi-arid environment (Tigray, Ethiopia). Plant and Soil 324:131-156.

Riginos C., Grace J.B., Augustine D.J., Young T.P., (2009) Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology 97:1337-1345.

Tainton N., Bransby D.I., Booysen P.d.V., (1990) Common veld and pasture grasses of Natal. Shuter and Shooter, Pietermaritzburg, South Africa.

Treydte A.C., Heitkonig I.M.A., Prins H.H.T., Ludwig F., (2007) Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology, Evolution and Systematics 8:197–205.

Valentin C., Poesen J., Li Y., (2005) Gully erosion: impacts, factors and control. Catena 63:132–153.

Van Auken O.W., (2009) Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931-2942.

Wiegand K., Ward D., Saltz D., (2005) Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. Journal of Vegetation Science 16:311-320.

Synthèse et conclusions

© N. Florsch

Collecte et transport de bois d'*Acacia* à Potshini.

Cette dernière partie synthétise l'ensemble des résultats présentés dans ce mémoire et répond aux questions posées en introduction. Une discussion est menée sur les apports de ce travail multidisciplinaire pour la gestion des pâturages envahis et des perspectives d'études complémentaires sont envisagées.

I. Apports scientifiques de l'étude sur les mécanismes de l'invasion ligneuse dans les pâturages ravinés

Ce travail a porté sur l'étude de l'invasion ligneuse dans un pâturage du piedmont du Nord du massif du Drakensberg de la province du KwaZulu Natal (Afrique du Sud) en lien notamment avec l'érosion en ravine. Quatre principales questions ont été formulées :

1) Comment l'invasion ligneuse et l'érosion en ravine ont-elles évolué à l'échelle du bassin versant au cours des 64 dernières années ? Notamment, comment l'hydrodynamique et les propriétés du sol interviennent-elles sur la répartition spatiale des acacias ?

L'analyse de photographies aériennes a permis d'étudier ce système à une large échelle temporelle et spatiale. La formation d'une savane à partir d'un pâturage originellement exclusivement composé par des espèces herbacées, a été possible en à peine 35 ans passant de 0 % de couvert arboré à 9,45 %. A la vue des taux d'invasion et des surfaces de couverts arborés observés dans la région, de 31 % au Swaziland (Roques et al. 2001) jusqu'à parfois 66 % de couvert arboré dans le district de Hlabisa près de Hluhluwe (Wigley et al. 2009), le pâturage de Potshini pourrait encore subir une forte augmentation de son couvert arboré.

L'érosion en ravine s'est révélée très importante avec un taux moyen de 200 Mg ha^{-1} an^{-1} reflétant les profondes ravines de cette région du KwaZulu-Natal. Les propriétés du sol et du sous-sol se sont avérées jouer un rôle important dans ce pâturage semi-humide semi-tropical. Les fortes teneurs en argile, tout particulièrement, peuvent limiter le développement des acacias et donc influencer leur répartition spatiale.

2) Comment les principaux facteurs de contrôle de l'invasion agissent-ils sur les premiers stades de la population d'*Acacia* ?

Cette question est primordiale pour la compréhension du système « arbre-herbe » des savanes. Nous avons pu mettre en évidence la prépondérance de l'influence de la strate herbacée sur la germination et la survie des plantules d'*Acacia sieberiana*. La strate herbacée, en compétition pour l'eau, les nutriments et la lumière avec les plantules est le principal facteur limitant le passage du stade plantule au stade jeune arbre dans ce système semi-humide. Ce résultat implique que des facteurs tels que le feu ou l'herbivorie réduisant le couvert herbacé ont un effet indirect positif important sur la survie des plantules. Nous avons aussi pu montrer que l'effet global des herbivores ne se limite pas à l'herbivorie et que le transit des graines d'acacia et les bouses de vaches peuvent contrebalancer en partie l'effet positif de l'herbivorie sur la survie des plantules. Les différences de résultats entre la serre et le terrain pour le facteur « transit digestif » montre une fois de plus les spécificités liées au terrain et la nécessité de mener de telles expériences à la fois en conditions contrôlées et en conditions naturelles. Cette étude a porté sur la germination et les plantules d'*A. sieberiana*, mais l'herbivorie et le feu peuvent aussi affecter les stades ultérieurs des populations ligneuses. Les résultats tirés de la littérature montrent des effets indirects positifs de l'herbivorie sur la croissance des arbres : un couvert herbacé réduit (affecté par l'herbivorie) permet une meilleure croissance des arbres à différents stades et notamment jusqu'au stade adulte (Riginos 2009). Au contraire, l'herbivorie peut limiter le développement de jeunes arbres par action directe de consommation des feuilles (Augustine et McNaugton 2004). Le feu peut également limiter la croissance de jeunes arbres ou d'arbres adultes si son intensité est suffisante (Bond et Keeley 2005). Le rôle des herbivores et du feu dans un tel système est donc ambivalent et nécessite des études plus approfondies prenant en compte les différents stades des populations ligneuses et les interactions existant entre ces deux facteurs de perturbations.

3) Quel est le lien entre la population d'*Acacia* et les ressources en eau du sol et particulièrement les profondeurs de prélèvement d'eau?

Nous avons montré que les acacias présentent des stratégies différentes de prélèvement de l'eau dans les différents horizons du sol en fonction de leur taille et de leur position dans la toposéquence. La séparation des niches selon le modèle à deux couches de Walter (1971) proposé dans l'équilibre du système « arbre-herbe » est une hypothèse réaliste dans cet écosystème notamment avec les acacias de grande taille qui pompent en profondeur. Le changement de profondeur de prélèvement de l'eau des jeunes acacias en fonction des saisons va dans le sens d'une diminution de la compétition interspécifique avec l'herbe et pourrait ainsi favoriser la survie et la croissance des jeunes acacias. Par conséquent, l'invasion par la population d'acacias pourrait être favorisée.

4) Quelles sont les conséquences de l'invasion ligneuse sur l'érosion en ravine et sur les propriétés du couvert herbacé et du sol?

Contrairement à ce qui est admis, les arbres ont été associés dans cette étude à une augmentation de l'érosion en ravine agissant probablement sur les processus de subsurface (comme par exemple une augmentation de l'infiltration de l'eau par écoulement le long des racines) en amont des ravines. Il a été parallèlement montré que ces ravines dépendent d'ailleurs principalement des mécanismes de subsurface et du gonflement-retrait des argiles provoquant la chute de blocs des flancs de ravines. En parallèle de cet effet sur l'extension des ravines, les arbres localisés dans les zones d'inter-ravines favorisent la présence de *Senecio inaequidens* sous leur canopée, plante toxique pour le bétail et les chevaux. C'est seulement dans les ravines que les arbres ont réellement montré un effet bénéfique en augmentant le couvert herbacé susceptible de maintenir le sol en place.

II. Implications de ces résultats pour la gestion des pâturages

Les résultats obtenus montrent l'importance de la spatialisation des acacias dans le pâturage et mettent en évidence les zones à considérer pour une gestion adaptée de ce type de pâturage. Comme il l'a été discuté dans la conclusion du chapitre 5 partie II, les premières mesures doivent porter sur le contrôle de la population de *Senecio inaequidens*. Ceci est possible par l'augmentation et la gestion du nombre de caprins et ovins qui pourraient aussi avoir un effet bénéfique sur le contrôle de la population d'acacias. En effet, les ovins et caprins ne sont pas sensible à la toxicité du *Senecio* et le consomment. Ils ont également un impact plus fort que le bétail sur les acacias par leur active consommation des feuilles d'acacias (Oates 1956, Dollahite 1972). En supposant que la population de *Senecio inaequidens* peut être contrôlée, les acacias ont globalement montré des effets positifs sur le couvert herbacé et sur les sols sous-canopée, tout particulièrement dans le fond des ravines. Cependant leur impact à grande échelle sur l'extension des ravines, lorsqu'ils sont localisés dans les zones de drainage des têtes de ravines n'est pas négligeable. A partir de ces informations, il est donc possible de prédire les zones prioritaires dans lesquelles une limitation de la densité d'acacias est souhaitée.

En utilisant une carte du réseau hydrique il est possible d'identifier les zones de drainage des têtes de ravines susceptibles de pouvoir évoluer (têtes de ravines actives) et de construire une carte des zones prioritaires à traiter (Fig. 1). Il est important de conserver les arbres dans les ravines car ils permettent de stopper l'exportation des sédiments, de créer des « îles » où la végétation herbacée pourra éventuellement recoloniser le milieu améliorant d'autant plus la stabilité du sol.

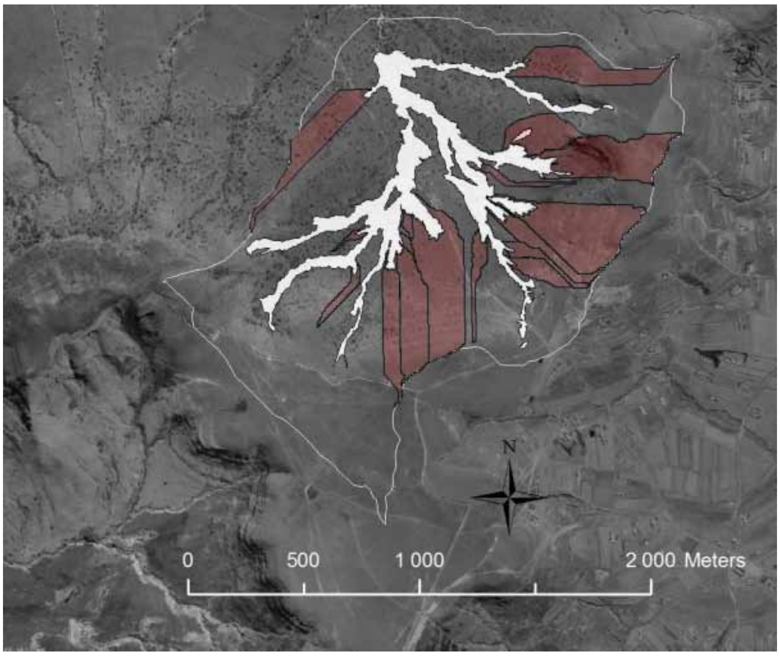


Figure 1. Carte des zones de drainage (en rouge) où les acacias sont susceptibles d'augmenter l'extension des têtes de ravines dans le pâturage de la communauté de Potshini.

L’impact du bétail est aussi important dans ce type d’écosystème et la protection des ravines contre le bétail pourrait favoriser la recolonisation des fonds de ravines par une végétation herbacée indispensable à la fixation du sol. Ainsi les surfaces de pâturage perdues en amont des ravines pourraient être en partie compensées par l’utilisation contrôlée des fonds de ravines.

Les techniques d’éclaircissement de la population ligneuse et de protection contre les herbivores sont bien documentées dans des ouvrages tels que *Veld Management in South Africa* par Tainton (1999). Le feu est très souvent employé pour limiter le développement des espèces ligneuses. Son utilisation est donc indispensable mais doit être contrôlée et les fréquences et intensités des feux modulées en fonction des spécificités du site. Il n’est pas évident que le feu seul, permette de maintenir des densités faibles de ligneux. Il faut plutôt regarder l’association du feu et du bétail. Une étude de Tainton (1999) sur 6 ans a montré que la présence de bovins sans application de feux augmentait de 64 % la densité d’arbres, alors qu’un traitement avec des feux (2 en 6 ans) et une charge légère continue de caprins ne modifiait pas la densité d’arbres. En parallèle de la gestion des feux et du bétail qui est indispensable au maintien durable des pâturages, des actions ponctuelles locales de coupe ou destruction d’arbres sont possibles par des méthodes physiques ou chimiques. Il est de toutes façons nécessaire de planifier une gestion à long terme de l’invasion ligneuse dans les pâturages car c’est un processus qui évolue dans le temps et qui, même s’il est contrôlé par des actions ponctuelles sera toujours une menace potentielle pour les pâturages. Dans le contexte actuel d’augmentation du dioxyde de carbone dans l’atmosphère, la coupe des arbres, connus pour stocker le carbone, n’est guère dans l’air du temps. Cependant, la perte des écosystèmes naturels de pâturages n’est pas seulement préjudiciable à l’homme en tant que ressource alimentaire pour le bétail, mais aussi à toute la faune et la flore sauvage très spécifique que les pâturages hébergent. De plus, il n’est pas évident que la présence d’arbres dans ces écosystèmes permette de réellement stocker le carbone, du moins cela dépendrait du climat : les zones envahies plus sèches montrent effectivement un stockage de carbone organique dans le sol tandis que les zones plus humides présentent au contraire une perte de carbone organique du sol (Jackson et al. 2002).

III. Perspectives

A partir de cette étude, plusieurs questions et thématiques de recherche futures peuvent être dégagées :

1) L'aspect spatial de l'invasion d'arbres n'a finalement été qu'abordé ici et la compréhension des processus de compétition intra-spécifique pourra être approfondie par des études à grande échelle temporelle et spatiale des populations de ligneux. C'est un des objectifs des travaux récemment entamés avec le Prof. Kerstin Wiegand.
2) L'association de différentes disciplines telle que l'écologie et la géophysique n'en est qu'à ses prémices. Toujours dans cette optique de large échelle (spatiale au moins), cette association pourra apporter de nombreuses réponses quant à la dynamique spatiale des populations ligneuses en fonction des propriétés du sol qui a encore été peu explorée. L'obtention de carte d'humidité des sols à large échelle est envisageable avec la géophysique. Il sera alors possible d'étudier comment la ressource en eau du sol modifie la répartition spatiale des arbres.
3) Les résultats montrant un effet positif des acacias sur l'extension des ravines amènent de nombreuses questions sur les mécanismes impliqués. Peut-on étendre ces résultats à d'autres zones ravinées et d'autres climats? Existe-t-il un lien entre le système racinaire des acacias et le réseau de drains internes « *pipes* » dans ce bassin versant? Quels sont les mécanismes prépondérants qui modifient l'hydrologie de surface ou subsurface en lien avec les arbres dans les pâturages? Cette dernière question fait intervenir les relations eau-sol-plantes pour lesquelles de nombreux aspects restent à étudier. Est-ce que d'autres acteurs jouant un rôle sur le sol, telles les termitières, peuvent aussi influencer les systèmes de drains de subsurface et accélérer l'érosion en ravine?
4) C'est aussi en comparant les sites, les espèces invasives, les climats, en réalisant des synthèses à l'échelle globale que l'on pourra déterminer plus finement les interactions entre les mécanismes régissant l'équilibre du système « arbre-herbe ». L'expérience de germination réalisée dans cette étude serait intéressante à répliquer dans différentes zones climatiques avec une prise en compte de plus de facteurs (intensité de feu, différentes charges d'animaux, etc.). Modéliser le système pourraient aussi être envisagé afin de prendre en compte les nombreux facteurs et acteurs d'un tel système et d'en extraire les processus importants. Dans ce cadre, les modèles matriciels où les différents stades de la population ligneuse peuvent être pris en compte de façon simple pourraient se révéler très utiles. Il s'agit d'un projet en cours avec Sébastien Barot pour lequel nous possédons toutes les données. La modélisation multi-agent pourrait aussi permettre une approche intéressante de ces systèmes impliquant de nombreux paramètres et interactions. Une intégration spatiale de la population est envisageable dans la modélisation multi-agent ainsi qu'une dimension sociale qui s'avère importante dans tout agro-écosystème. Ces modèles pourraient constituer la base d'un outil d'aide à la décision où les effets des différents agents/acteurs/facteurs peuvent être simulés pour prédire des évolutions à long terme du pâturage en fonction de la gestion en cours.

Bibliographie

Abule E., Smit G.N., Snyman H.A., (2005) The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the Middle Awash Valley of Ethiopia. Journal of Arid Environments 60:343-358.

Archer S., Boutton T.W., Hibbard K.A., (2001) Trees in grasslands: biogeochemical consequences of woody plant expansion. In: Schulze E.-D., Heimann M., Harrison S., Holland E., Lloyd J., Prentice I.C., Schimel D. Global Biogeochemical Cycles in the Climate System, pp.115-138. Academic Press, San Diego.

Archer S., Schimel D.S., Holland E.A., (1995) Mechanisms of shrubland expansion: Landuse, climate or $CO_{2.}$ Climate Change 29:91-95.

Asner G.P., Elmore A.J., Olander L.P., Martin R.E., Harris A.T., (2004) Grazing systems, ecosystem responses, and global change. Annual Review of Environment and Resources 29:261-299.

Augustine D.J., McNaughton S.J., (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology 41:45-58.

Beckedahl H.R., (1998) Subsurface soil erosion phenomena in South Africa. pp.128. Justus Perthes Verlag Gotha, Germany.

Belsky A.J., Amundson R.G., Duxbury J.M., Riha S.J., Ali A.R., Mwonga S.M., (1989) The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26:1005-1024.

Bond W.J., (2008) What limits trees in C_4 grasslands and savannas? Annual Review of Ecology, Evolution and Systematics 39:641-659.

Bond W.J., Keeley J.E., (2005) Fire as a global `herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution 20:387-394.

Bonnet O., Fritz H., Gignoux J., Meuret M., (2010) Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. Journal of Ecology 98:908-916.

Botha G.A., Wintle A.G., Vogel J.C., (1994) Episodic late Quaternary palaeogully erosion in northern KwaZulu-Natal, South Africa. Catena 23:327-340.

Bouchnak H., Felfoul M.S., Boussema M.R., Snane M.H., (2009) Slope and rainfall effects on the volume of sediment yield by gully erosion in the Souar lithologic formation (Tunisia). Catena 78:170-177.

Briggs J.M., Knapp A.K., Blair J.M., Heisler J.L., Hoch G.A., Lett M.S., McCarron J.K., (2005) An ecosystem in transition: causes and consequences of the conversion of mesic grassiand to Shrubland. BioScience 55:243-254.

Britz M.-L., Ward D., (2007) Dynamics of woody vegetation in a semi-arid savanna, with a focus on bush encroachment. African Journal of Range & Forage Science 24:131-140.

Brown J., Scholtz C.H., Janeau J.-L., Grellier S., Podwojewski P., (2010) Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties. Applied Soil Ecology 46:9-16.

Bull W.B., (1981) Soils, geology, and hydrology of deserts. In: Evans, D.D. and Thames, J.L. (Eds), Water in desert ecosystems, pp. 42–58, Stroudsberg PA: Dowden, Hutchinson and Ross.

Callaway R.M., Walker L.R., (1997) Competition and facilitation: A synthetic approach to interactions in plant communities. Ecology 78:1958-1965.

Carlyle-Moses D.E., (2004) Throughfall, stemflow, and canopy interception loss fluxes in a semi-arid Sierra Madre Oriental matorral community. Journal of Arid Environments 58:181-202.

Casenave A., Valentin C., (1992) A runoff capability classification system based on surface features criteria in the arid and semi-arid areas of West Africa. Journal of Hydrology 130:213-249.

Coe M., Coe C., (1987) Large herbivores, acacia trees and bruchid beetles. South African Journal of Science 83:624-635.

Cramer M.D., Chimphango S.B.M., Cauter A.V., Waldram M.S., Bond W.J., (2007) Grass competition induces N_2 fixation in some species of African *Acacia*. Journal of Ecology 95:1123–1133.

Descroix L., Viramontes D., Vauclin M., Barrios J.L.G., Esteves M., (2001) Influence of soil surface features and vegetation on runoff and erosion in the western Sierra Madre (Durango, Northwest Mexico). Catena 43:115-135.

Dollahite J.W., (1972) The use of sheep and goats to control *Senecio* poisoning in cattle. Southwest Veterinary 25:223-226.

Dunkerley D.L., (2002) Infiltration rates and soil moisture in a groved mulga community near Alice Springs, arid central Australia: evidence for complex internal rainwater redistribution in a runoff-runon landscape. Journal of Arid Environments 51:199-219.

Eagleson P.S., Segara R.I., (1985) Water-limited equilibrium of savanna vegetation systems. Water Resources Research 21:1483-1493.

Eggemeyer K.D., Awada T., Harvey E.F., Wedin D.A., Zhou X., Zanner W.C., (2008) Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C_4 grasses in a semiarid grassland. Tree Physiology 29:157-169.

Ehleringer J.R., (2005) The influence of atmospheric CO2, temperature, and water on the abundance of C3/C4 taxa. in: Ehleringer J.R., Cerling, T.E., Dearing, M.D. A history of atmospheric CO_2 and its effects on plants, animals, and ecosystems, pp.214–231. Springer, New York.

Fornara D., du Toit J., (2008) Community-level interactions between ungulate browsers and woody plants in an African savanna dominated by palatable-spinescent *Acacia* trees. Journal of Arid Environments 72:534-545.

Fuhlendorf S.D., Archer, S.R., Smeins, F.E., Engle, D.M., Taylor, C.A., (2008) The combined influence of grazing, fire, and herbaceous productivity on tree–grass interactions. In: Van Auken O.W. Western North American Juniperus Communities: A Dynamic Vegetation Type, pp.219–238. Springer, New York.

Fynn R.W.S., Morris C.D., Edwards T.J., (2005) Long-term compositional responses of a South African mesic grassland to burning and mowing. Applied Vegetation Science 8:5-12.

Gignoux J., Lahoreau G., Julliard R., Barot S., (2009) Establishment and early persistence of tree seedlings in an annually burned savanna. Journal of Ecology 97:484-495.

Goheen J.R., Keesing F., Allan B.F., Ogada D., Ostfeld R.S., (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. Ecology 85:1555-1561.

Goheen J.R., Palmer T.M., Keesing F., Riginos C., Young T.P., (2010) Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal Ecology 79:372-382.

Graz F.P., (2008) The woody weed encroachment puzzle: gathering pieces. Ecohydrology 1:340-348.

Guy R.M., Smith J.M.B., (1995) A land potential classification for KwaZulu-Natal. Report number N/A/95/12, KwaZulu-Natal Department of Agriculture, Cedara, South Africa.

Gyssels G., Poesen J., (2003) The importance of plant root characteristics in controlling concentrated flow erosion rates. Earth Surface Processes and Landforms 28:371-384.

Higgins S.I., Bond W.J., Trollope W.S.W., (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. Journal of Ecology 88:213-229.

Hoffman T., Ashwell A., (2001) Nature divided, land degradation in South Africa. University of Cape Town Press, Cape Town, South Africa.

House J.I., Archer S., Breshears D.D., Scholes R.J., (2003) Conundrums in mixed woody–herbaceous plant systems. Journal of Biogeography 30:1763-1777.

Huxman T.E., Wilcox B.P., Breshears D.D., Scott R.L., Snyder K.A., Small E.E., Hultine K., Pockman W.T., Jackson R.B., (2005) Ecohydrological implications of woody plant encroachment. Ecology 86:308-319.

Imeson A.C., Kwaad F.J.P.M., (1980) Gully types and gully prediction. K.N.A.G. Geografisch Tijdschrift XIV 5:430-441.

Jackson R.B., Banner J.L., Jobbágy E.G., Pockman W.T., Wall D.H., (2002) Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623-626.

Jeltsch F., Milton S.J., Dean W.R.J., Van Rooyen N., (1996) Tree spacing and coexistence in semiarid savannas. Journal of Ecology 84:583-595.

Jeltsch F., Milton S.J., Dean W.R.J., van Rooyen N., Moloney K.A., (1998) Modelling the impact of small-scale heterogeneities on tree-grass coexistence in semi-arid savannas. Journal of Ecology 86:780-793.

Jeltsch F., Weber G.E., Grimm V., (2000) Ecological buffering mechanisms in savannas: a unifying theory of long-term treegrass coexistence. Plant Ecology 161:161-171.

Joffe P., (2003) *Acacia sieberiana*. Pretoria National Botanical Garden, South African National Biodiversity Institute, South Africa. http://www.plantzafrica.com/plantab/acaiasieber.htm, accédée le 04 avril 2011.

Kambatuku J.R., Cramer M.D., Ward D., (in press) Intraspecific competition between shrubs in a semi-arid savanna. Plant Ecology.

King G.M., (2002) An explanation of the 1:500 000 general hydrogeological map. Department of Water Affairs and Forestry, Pretoria, South Africa.

Knapp A.K., Briggs J.M., Collins S.L., Archer S.R., Bret-Harte M.S., Ewers B.E., Peters D.P., Young D.R., Shaver G.R., Pendall E., Cleary M.B., (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Global Change Biology 14:615-623.

Kongo M.V., Jewitt W.P.G., (2006) Preliminary investigation of catchment hydrology in response to agricultural water use innovations: a case study of Potshini catchment-South Africa. Physics and chemistry of the Earth 37:976-987.

Kraaij T., Ward D., (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. Plant Ecology 186:235-246.

Lal R., (1998) Soil erosion impact on agronomic productivity and environment quality. Critical Review Plant Science 17:319-464.

Roux J.J.L., Newby T.S., Sumner P.D., (2007) Monitoring soil erosion in South Africa at a regional scale: review and recommendations. South African Journal of Science 103:329-335.

Lett M.S., Knapp A.K., (2003) Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. Journal of Vegetation Science 14:487-496.

Liang W.-L., Kosugi K., Mizuyama T., (2009) A three-dimensional model of the effect of stemflow on soil water dynamics around a tree on a hillslope. Journal of Hydrology 366:62-75.

Ludwig F., Dawson T.E., de Kroon H., Berendse F., Prins H.H.T., (2003) Hydraulic lift in *Acacia tortilis* trees on an East African savanna. Oecologia 134:293–300.

Ludwig F., de Kroon H., Berendse F., Prins H.H.T., (2004) The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecology 170:93–105.

Ludwig F., de Kroon H., Prins H.H.T., (2008) Impacts of savanna trees on forage quality for a large African herbivore. Oecologia 155:487–496.

Ludwig J., Wilcox B., Breshears D., Tongway D., Imeson A., (2005) Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology 86:288-297.

Martin S., Morton H., (1993) Mesquite control increases grass density and reduces soil loss in Southern Arizona. Journal of Range Management 46:170-175.

Martinez-Casasnovas J., Ramos M., Garcia-Hernandez D., (2009) Effects of land-use changes in vegetation cover and sidewall erosion in a gully head of the Penedes region (northeast Spain). Earth Surface Processes and Landforms 34:1927-1937.

Martinez-Meza E., Whitford W.G., (1996) Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. Journal of Arid Environments 32:271-287.

Mauchamp A., Janeau J.L., (1993) Water funnelling by the crown of *Flourensia cernua*, a Chihuahuan desert shrub. Journal of Arid Environments 25:299-306.

Mbatha K.R., Ward D., (2010) The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. Journal of Arid Environments 74:1294-1301.

McCole A.A., Stern L.A., (2007) Seasonal water use patterns of *Juniperus ashei* on the Edwards plateau, Texas, based on stable isotopes in water. Journal of Hydrology 342:238-248.

Meyer K.M., Wiegand K., Ward D., Moustakas A., (2007) SATCHMO: A spatial simulation model of growth, competition, and mortality in cycling savanna patches. Ecological Modelling 209:377-391.

Miriti M., (2006) Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973-979.

Mucina L., Rutherford M.C., (2006) The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa.

Mudhara M., Malinga, M. Salomoni, (submitted) Enhancing farmers innovative capacity in soil and water mangement through participatory action research in Potshini, South Africa. Physics and Chemistry of the Earth.

Muñoz-Robles C., Reid N., Frazier P., Tighe M., Briggs S.V., Wilson B., (2010) Factors related to gully erosion in woody encroachment in south-eastern Australia. Catena 83:148-157.

Muñoz-Robles C., Reid N., Tighe M., Briggs S.V., Wilson B., (2011) Soil hydrological and erosional responses in patches and inter-patches in vegetation states in semi-arid Australia. Geoderma 160:524-534.

Neave M., Rayburg S., (2007) A field investigation into the effects of progressive rainfall-induced soil seal and crust development on runoff and erosion rates: The impact of surface cover. Geomorphology 87:378-390.

Oates A.V., (1956) Goats as a possible weapon in the control of the thorn bush. Rhodesia Agricultural Journal 53-68.

Ojima D.S., Galvin K.A., Turner B.L., (1994) The global impact of land-use change. Bioscience 44:300-304.

Or K., Ward D., (2007) Maternal effects on the life histories of bruchid beetles infesting *Acacia raddiana* in the Negev desert, Israel. Entomologia Experimentalis et Applicata 122:165-170.

Oudtshoorn F.V., (2004) Guide to grasses of Southern Africa. Briza Publications, Pretoria, South Africa.

Petersen S.L., Stringham T.K., (2008) Infiltration, runoff, and sediment yield in response to western juniper encroachment in southeast Oregon. Rangeland Ecology & Management 61:74-81.

Podwojewski P., Janeau J.L., Grellier S., Valentin C., Lorentz S., Chaplot V., (in Press) Influence of vegetal soil cover on water runoff and soil detachment in a sub-humid South African degraded rangeland. Earth Surface Processes and Landforms.

Poesen J., Nachtergaele J., Verstraeten G., Valentin C., (2003) Gully erosion and environmental change: importance and research needs. Catena 50:91-133.

Pooley E., (1993) The complete guide to trees of Natal, Zululand and Transkei. Natal Flora Publications Trust, Durban, South Africa.

Ravi S., D'Odorico P., Huxman T.E., Collins S.L., (2010) Interactions between soil erosion processes and fires: implications for the dynamics of fertility islands. Rangeland Ecology and Management 63:267-274.

Reid K., Wilcox B., Breshears D., MacDonald L., (1999) Runoff and erosion in a pinon-juniper woodland: influence of vegetation patches. Soil Science Society of America Journal 63:1869-1879.

Reinsch S., Schleicher J., Trinogga J., Ward D., Wiegand K., Geilmann H., Bartram S., (in prep) Differences in water uptake strategies of two competing savanna woody species. Oecologia

Reynolds J.F., Smith D.M.S., Lambin E.F., Turner B.L., Mortimore M., Batterbury S.P.J., Downing T.E., Dowlatabadi H., Fernandez R.J., Herrick J.E., Huber-Sannwald E., Jiang H., Leemans R., Lynam T., Maestre F.T., Ayarza M., Walker B., (2007) Global desertification: building a science for dryland development. Science 316:847-851.

Riginos C., (2009a) Grass competition suppresses savanna tree growth across multiple demographic stages. Ecology 90:335–340.

Riginos C., Grace J.B., Augustine D.J., Young T.P., (2009b) Local versus landscape-scale effects of savanna trees on grasses. Journal of ecology 97:1337-1345.

Robinson D.A., Abdu H., Jones S.B., Seyfried M., Lebron I., Knight R., (2008) Eco-geophysical imaging of watershed-scale soil patterns links with plant community spatial patterns. Vadose Zone Journal 7:1132-1138.

Roques K.G., O’Connor T.G., Watkinson A.R., (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280.

Ruthven D.C., (2001) Herbaceous vegetation diversity and abundance beneath honey mesquite (*Prosopis glandulosa*) in the South Texas plains. Texas Journal of Science 53:171-186.

Samani A.N., Ahmadi H., Mohammadi A., Ghoddousi J., Salajegheh A., Boggs G., Pishyar R., (2010) Factors controlling gully advancement and models evaluation (Hableh Rood Basin, Iran). Water Resources Management 24:1531-1549.

Sankaran M., Hanan N.P., Scholes R.J., Ratnam J., Augustine D.J., Cade B.S., Gignoux J., Higging S.I., Roux X.L., Ludwig F., Ardo J., Banyikwa F., Bronn A., Bucini G., Caylor K.K., Coughenour M.B., Diouf A., Ekaya W., Feral C.J., February E.C., Frost P.G.H., Hiernaux P., Hrabar H., Metzger K.L., Prins H.H.T., Ringrose S., Sea W., Tews J., Worden J., Zambatis N., (2005) Determinants of woody cover in African savannas. Nature 438:846-849.

Sankaran M., Ratnam J., Hanan N., (2008) Woody cover in African savannas: the role of resources, fire and herbivory. Global Ecology and Biogeography 17:236-245.

Sankaran M., Ratnam J., Hanan N.P., (2004) Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters 7:480-490.

Scholander P.F., Hammel H.T., Bradstreet E.D., Hemmingsen E.A., (1965) Sap pressure in vascular plants. Science 148:339-346.

Scholes R.J., Archer S.R., (1997) Tree-grass interactions in savannas. Annual Review of Ecology and Systematics 28:517-544.

Schulze R.E., (1997) South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria, South Africa.

Sher A.A., Wiegand K., Ward D., (2010) Do *Acacia* and *Tamarix* trees compete for water in the Negev desert? Journal of Arid Environments 74:338-343.

Simmons M.T., Archer S.R., James Ansley R., Teague W.R., (2007) Grass effects on tree (*Prosopis glandulosa*) growth in a temperate savanna. Journal of Arid Environments 69:212-227.

Smit G.N., (2004) An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. Journal of Environmental Management 71:179-191.

Tainton N., (1999) Veld management in South Africa. University of KwaZulu-Natal, Scottsville, South Africa.

Tisdale S.L., Nelson W.L., Beaton J.D., Havlin J.L., (1993) Soil fertility and fertilizers, 5th ed. Macmillan Publishing Company, New York, NY, US.

Treydte A.C., Heitkonig I.M.A., Prins H.H.T., Ludwig F., (2007) Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology, Evolution and Systematics 8:197–205.

Trinogga J., (2010) Arid savanna shrubs affect soil chemistry and vegetation cover. School of Biology and Pharmacy, Master thesis. Friedrich Schiller University, Jena, Germany.

Trollope W.S.W., (1980) Controlling bush encroachment with fire in the savanna areas of South Africa. Proceedings of the Grassland Society of South Africa 15:173-177.

Valentin C., Poesen J., Li Y., (2005) Gully erosion: impacts, factors and control. Catena 63:132–153.

Van Auken O.W., (2009) Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management 90:2931-2942.

Van Langevelde F., Van de Vijver C.A.D.M., Kumar L., Van de Koppel J., De Ridder N., Van Andel J., Skidmore A.K., Hearne J.W., Stroosnijder L., Bond W.J., Prins H.H.T., Rietkerk M., (2003) Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84:337-350.

Vandekerckhove L., Poesen J., Wijdenes D.O., Gyssels G., Beuselinck L., de Luna E., (2000) Characteristics and controlling factors of bank gullies in two semi-arid mediterranean environments. Geomorphology 33:37-58.

Verachtert E., M. Van Den Eeckhaut, Poesen J., Deckers J., (2010) Factors controlling the spatial distribution of soil piping erosion on loess-derived soils: a case study from central Belgium. Geomorphology 118:339-348.

Vetaas O.R., (1992) Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science 3:337-344.

Walter H., (1971) Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, UK.

Ward D., (2005) Do we understand the causes of bush encroachment in African savannas? African Journal of Range & Forage Science 22:101-105.

Ward D., (2010) A resource ratio model of the effects of changes in CO_2 on woody plant invasion. Plant Ecology 209:147-152.

Ward D., Feldman, K., Avni, Y., (2001) The effects of loess erosion on soil nutrients, plant diversity and plant quality in Negev desert wadis. Journal of Arid Environments 48:461-473.

Wiegand K., Saltz D., Ward D., (2006) A patch-dynamics approach to savanna dynamics and woody plant encroachment – Insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7:229-242.

Wiegand K., Ward D., Saltz D., (2005) Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer. Journal of Vegetation Science 16:311-320.

Wigley B.J., Bond W.J., Hoffman M.T., (2009) Bush encroachment under three contrasting land-use practices in a mesic South African savanna. African Journal of Ecology 47:62–70.

Wilson J.B., (1988) Shoot competition and root competition. Journal of Applied Ecology 25:279-296.

World Resources Institute, http://www.wri.org/publication/content/8269, accedé le 19 avril 2011.

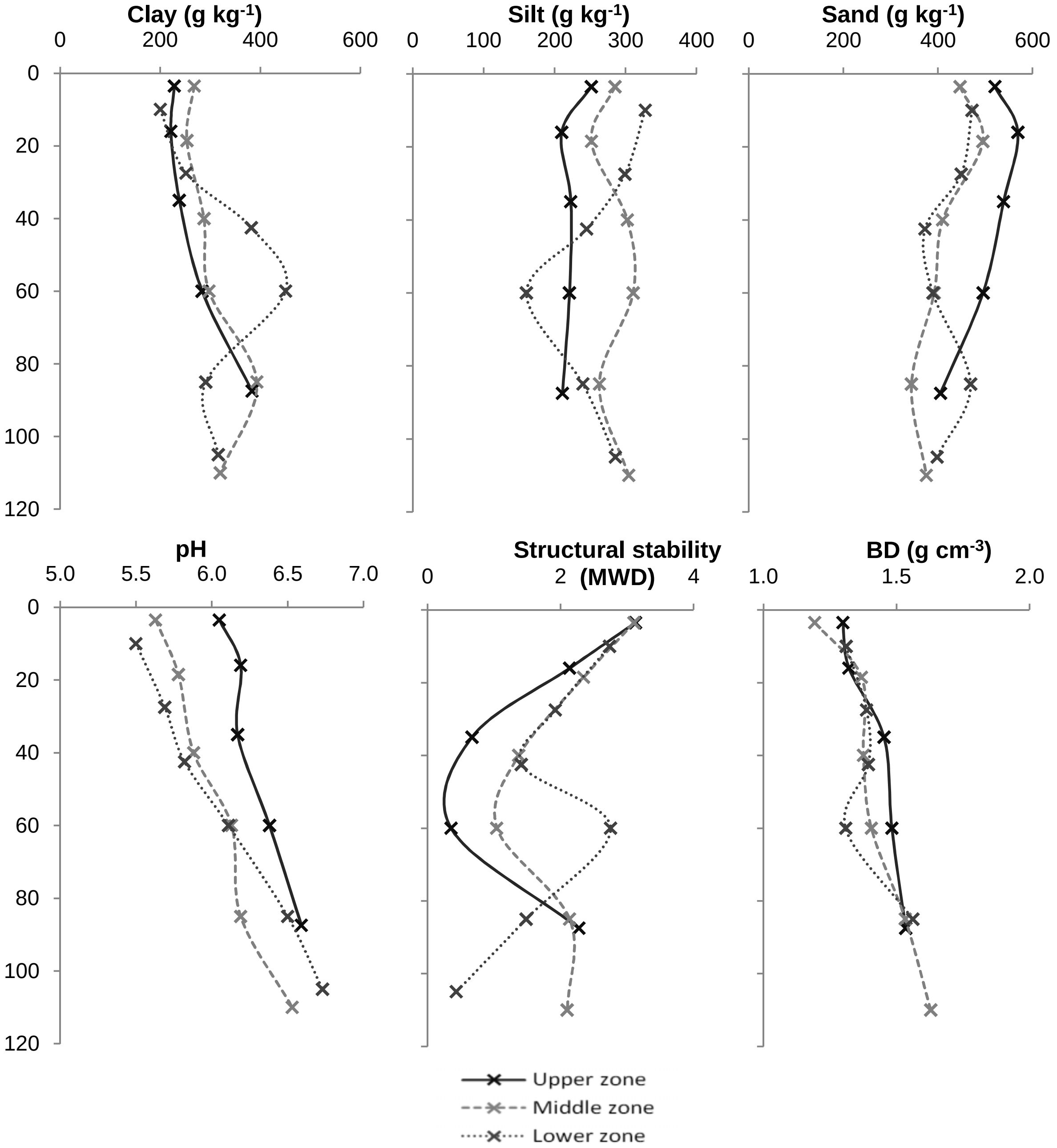
Yaalon D.H., (1987) Is gullying associated with highly sodic colluvium? Further comment to the environmental interpretation of southern African dongas. Palaeogeography, Palaeoclimatology, Palaeoecology 58:121-123.

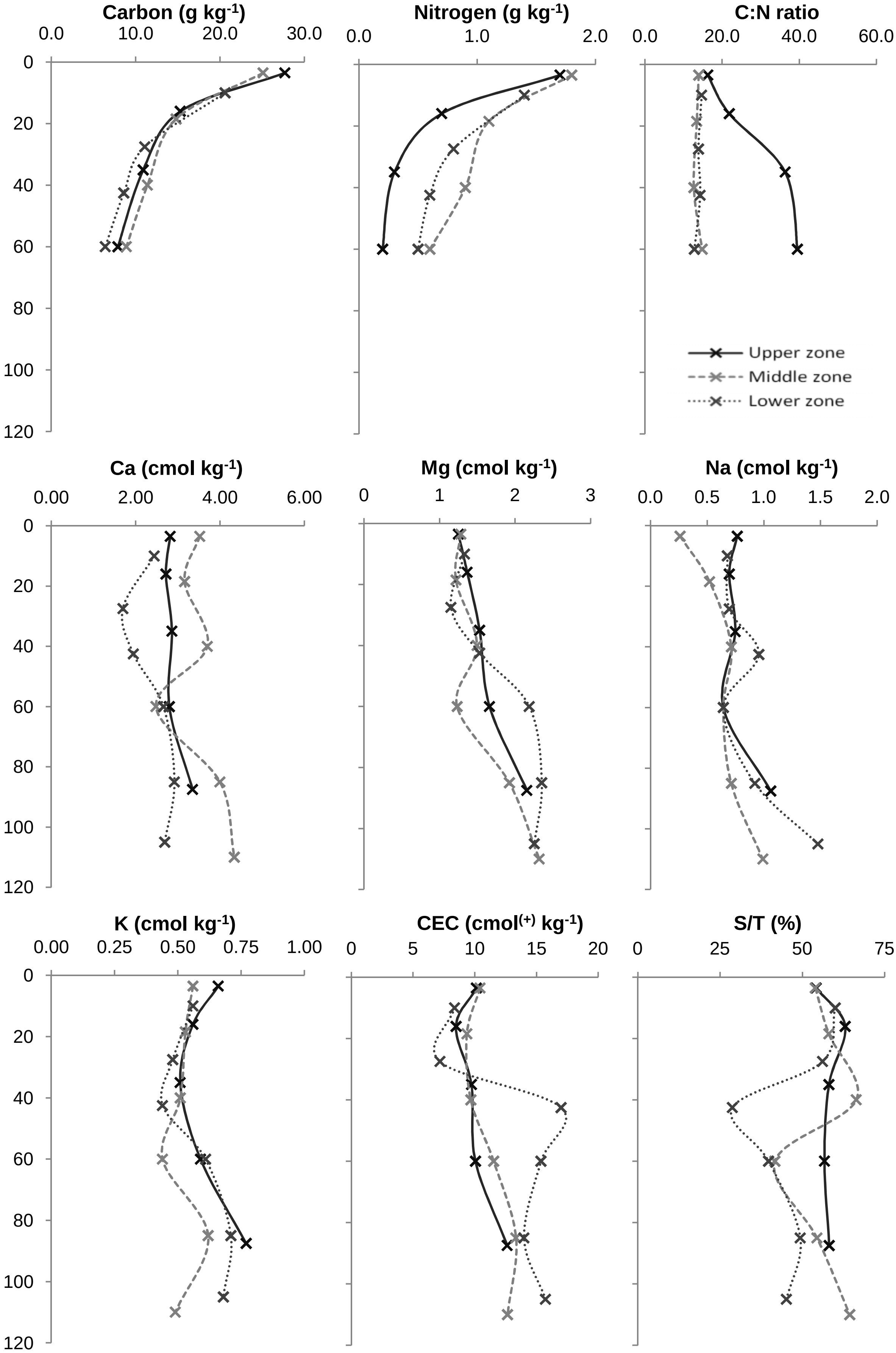
Zacharias P., (1986) The use of the cellulase digestion procedure for indexing the dry matter digestibility of forages. African Journal of Range & Forage Science 3:117-121.

ANNEXES

Annexe 1. Résultats des analyses de trois profils de sol

Résultats de l’analyse des principaux parameters physico-chimiques de trois profils de sol localisés en haut, milieu et bas de versant (Upper, Middle, Lower).




Carbon (g kg-1)
0.0
10.0
20.0
30.0
Nitrogen (g kg-1)
0.0
1.0
2.0
C:N ratio
0.0
20.0
40.0
60.0
0
20
40
60
80
100
120
Upper zone
Middle zone
Lower zone
Ca (cmol kg-1)
0.00
2.00
4.00
6.00
Mg (cmol kg-1)
0
1
2
3
Na (cmol kg-1)
0.0
0.5
1.0
1.5
2.0
K (cmol kg-1)
0.00
0.25
0.50
0.75
1.00
CEC (cmol(+) kg-1)
0
5
10
15
20
S/T (%)
0
25
50
75

Annexe 2. Résumé de l’article accepté dans *Soil Applied Ecology*

Dung beetles (Coleoptera: Scarabaeidae) can improve soil hydrological properties

Jacqueline Brown[a], Clarke H. Scholtz[a], Jean-Louis Janeau[b], Seraphine Grellier[b], Pascal Podwojewski[b]

[a]*Department of Zoology and Entomology, University of Pretoria, Lynnwood Road, Hatfield, Pretoria, Gauteng, 0002, SouthAfrica*
[b]*Institut de Recherche pour le Developpement c/o School of Bioresources Engineering and Environmental Hydrology, University of KwaZulu-Natal, Scottsville, 3209, SouthAfrica*

Received 26 January 2010, Received in revised form 24 May 2010, Accepted 26 May 2010.

Abstract

Although dung beetles are known to perform a multitude of ecosystem services, their effects on water infiltration, runoff, porosity, moisture and erosion of soil have never been thoroughly researched. Maintenance of these hydrological properties is important in agro-ecosystem functioning where overgrazing results in negative impacts on the soil. The study site was located in the Potshini catchment in Kwazulu-Natal (South Africa), an area heavily grazed by livestock. We conducted two rainfall simulations on three 1 m^2 control (no dung) and six dung-treated plots in December 2008, and repeated the study in June 2009 on the same plots. Natural populations of dung beetles were all owed to colonise the dung. Simulations were conducted for 30 min at an intensity of 30 mm h^{-1}. Key variables calculated were pre-runoff amounts (Pi), infiltration ratios (Ki), and soil losses. Samples were collected for bulk density determination during the same time periods in order to measure differences in porosity and moisture in control and dung-treated plots at different depths. Using multivariate statistics we found significant differences between dung-treated and control plots in three of four simulations. After 48 h of beetle activity, Pi and Ki values were significantly increased and remained at elevated levels six months later. Soil losses were initially higher in dung-treated plots than controls, but had declined to less than control values after six months. Bulk density in the A-horizon (0–10 cm) was significantly reduced after 48 h of beetle activity and remained so for six months. No difference in bulk density was observed at greater depths. Soil moisture initially increased significantly in the A-horizon, as well as at 20 and 30 cm depths after six months of activity. We conclude that dung beetles positively influence hydrological properties of the soil by increasing water infiltration and soil porosity, and reducing surface water runoff. Contrasting effects on soil losses are problematic to reconcile from this study. High losses initially observed may be offset in the long-term by reductions associated with the increased infiltration ratios, though this remains to be confirmed.

Annexe 3. Résumé de l'article accepté dans *Earth Surface Processes and Landforms*

Influence of grass soil cover on water runoff and soil detachment under rainfall simulation in a sub-humid South African degraded rangeland

Pascal Podwojewski[a], Jean Louis Janeau[a], Séraphine Grellier[a], Christian Valentin[c], Simon Lorentz[b] and Vincent Chaplot[a]

[a]*IRD, UMR Bioemco c/o School of Bioresources Engineering and Environmental Hydrology–Rabie Saunders Building, University of KwaZulu-Natal, Scottsville 3209, South Africa*
[b]*School of Bioresources Engineering and Environmental Hydrology Rabie Saunders Building, University of Kwazulu-Natal, Scottsville 3209, South Africa*
[c]*IRD, UMR Bioemco, Centre IRD d'Île de France 32, avenue Henri Varagnat, 93143 Bondy Cedex, France*

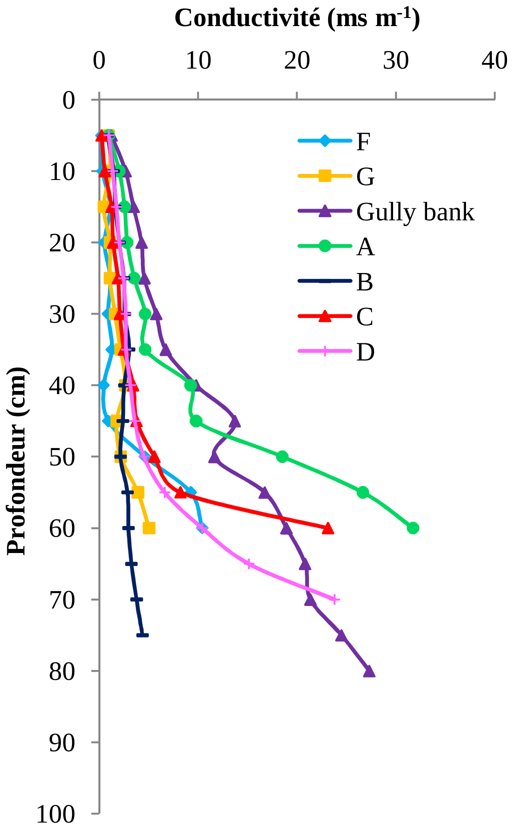
Received 7 May 2010; Revised 8 November 2010; Accepted 15 November 2010

Abstract

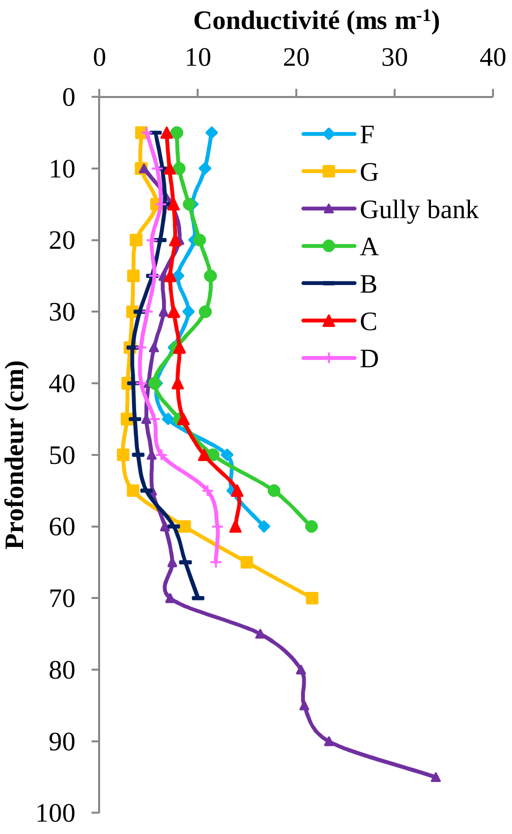
In most regions of the world overgrazing plays a major role in land degradation and thus creates a major threat to natural ecosystems. Several feedbacks exist between overgrazing, vegetation, soil infiltration by water and soil erosion that need to be better understood. In this study of a sub-humid overgrazed rangeland in South Africa, the main objective was to evaluate the impact of grass cover on soil infiltration by water and soil detachment. Artificial rains of 30 and 60 mm h^{-1} were applied for 30 min on 1 m^2 micro-plots showing similar sandy-loam Acrisols with different proportions of soil surface coverage by grass (Class A: 75–100%; B: 75–50%; C: 50–25%; D: 25–5%; E: 5–0% with an outcropping A horizon; F: 0% with an outcropping B horizon) to evaluate pre-runoff rainfall (Pr), steady state water infiltration (I), sediment concentration (SC) and soil losses (SL). Whatever the class of vegetal cover and the rainfall intensity, with the exception of two plots probably affected by biological activity, I decreased regularly to a steady rate <2 mm h^{-1} after 15 min rain. There was no significant correlation between I and Pr with vegetal cover. The average SC computed from the two rains increased from 0·16 g L^{-1} (class A) to 48·5 g L^{-1} (class F) while SL was varied between 4 g m^{-2} h^{-1} for A and 1883 g m^{-2} h^{-1} for F. SL increased significantly with decreasing vegetal cover with an exponential increase while the removal of the A horizon increased SC and SL by a factor of 4. The results support the belief that soil vegetation cover and overgrazing plays a major role in soil infiltration by water but also suggest that the interrill erosion process is self-increasing. Abandoned cultivated lands and animal preferred pathways are more vulnerable to erosive processes than simply overgrazed rangelands.

Annexe 4. Mesure de conductivités électriques sur plusieurs profils de sol

Diagraphie de conductivités en
juin 2010 (saison sèche)



Diagraphie de conductivités en
février 2010 (saison humide)



Annexe 5. Principe de l’inversion bayésienne sur les mesures de l’EM38-MK2

Bayesian inversion of Slingram EM38 data for topsoil and subsoil geoelectrical characterisation

Nicolas Florsch, Séraphine Grellier, Jean-Louis Janeau, Pascal Podwojewski,
Christian Camerlynck, Simon Lorentz

Keywords: EM38, duplex soil, inversion, bayesian

Cette annexe ainsi que l’annexe 6 font parties d’un article méthodologique sur l’inversion bayésienne en cours de préparation.

1. Introduction

Slingram methods are widely used to characterize the first soil horizons, thanks to the fact that the soil layer involved changes in the conductivity which is the target of this inductive electromagnetic method. Among the available devices, the EM38 and the new EM38-MK2 from Geonics involve scales that match the common first soil layer (Corwin and Lesch 2005). A very informative documentation on the instrument and Slingram in general is provided by GEONICS in their Technical Note n°6, “TN6”, that is available on line for a long time (Mc Neill 1980). The EM38 involves a 1-m coil spacing (1 transmitter coil and one receiver coil) while the EM38-MK2 has three coils (1 transmitter and two receivers) and involves two spacings: 1 m and 50 cm. Geonics also market apparatus with 2 m (EM31-SH), 3.66 m (EM31), 10, 20 and 40 m (EM34). Other brands propose equivalent systems, like (DUAMLEM, see for instance Saey, 2009), which are also used for shallow investigations. Abdu et al. (2007) compares the EM38 and the DUALEM-1S.

The Slingram method is very popular because it allows fast measurements of electrical conductivity EC (no galvanic contact required), and it can be used for several purposes. EC is a major parameter available from geophysics and depends of soil parameter that draws attention to soil scientists and environmentalists. It is used to assess soil salinity processes (Rhoades et al. 1989, McNeill 1992, Williams and Baker 1982, Sudduth et al. 2001, Lesch et al. 1995), for example in precision agriculture (Lund et al. 1999, Mueller et al. 2003, Sudduth et al. 2001, Kitchen el al. 2005), or for geomorphologic and sedimentation purposes (Saey et al. 2008, Kitchen et al. 1996), and is useful to characterize the water content (Hanson and Kaita 1997; Hezarjaribi and Sourell H. 2007; Kachanoski 1990; Khakural et al. 1998; Brevik et al. 2006; Sherlock and McDonnell 2003) or/and clay content (Cockx et al. 2007, Doolittle et al. 1994, Kitchen et al. 1999). Slingram contributes to the study of the interaction between plants and soils through the conductivity (Myers et al. 2007; Hossain et al. 2010).

Depending on the user requirements, the data can be used in a qualitative mode, for instance to delineate specific areas (salted or clayey areas for instance) or in a quantitative mode, in which quantitative parameters are to be determined. This case involves the determination of the conductivity of a given layer (or area) to be converted into hydrological parameter (water content, clay amount) and also the geometrical organization of the soil, in terms of thicknesses of the first layers. In the first case, the survey is rapid and do not involve accurate conductivity determination. In the second case, a high attention must be paid to the field procedure and data post-processing, due to the main drawback of the slingram: the drift.

The drift is inherent to the apparatus configuration. Precisely, the secondary field only, generated within the ground, is proportional to the ground conductivity, but the receiving coil also intercepts the flux of the primary field, much stronger than the field resulting from the induction in the ground. This primary field is compensated electronically, but is prone to the electronic drifts due to temperature dependence of the in-built semi-conductors, the battery voltage decrease and the device stand deformation (of thermal origin too). Robinson et al.

(2004) provided a study on the EM38 drift, and Sudduth et al. (2001) proposes a procedure to reduce its effects, in a paper devoted to precision agriculture.

The drift is a default in compensating the primary field and is an additive effect, although it is not an amplitude compensation, but a delicate phase adjustment of the in-phase in quadrature signals separation. It is strong just after the device has been turned on, and it is necessary to wait a few minutes prior to acquire data, for electronic thermal stabilization. Then the most sensitive effect is due to the direct sun exposure, and it is much better to remain aligned with the sun that varying the orientation of the stand. Working during cloudy condition is much better.

In our experience, the drift of the EM38 can reach tens of mS m^{-1} within one hour. For the EM38-MK2, the drift has been reduced effectively to 1 or 2 mS m^{-1} for the same duration, as far as the 1m spacing is concerned. The 50 cm spacing behaves like the 1 m spacing of the older device. How to manage the drift is discussed further in the paper.

The Slingram device measurement integrates the ground conductivity below the instrument as described by McNeill in his reference paper (1980). Actually Slingram can be used for 3-D structure targeting like in mining, or to characterize the geoelectrical parameters of a layered medium, typically the first soil horizons. In the present paper, we only deal with the second kind of objective and we are only concerned by the 1-D conductivity dependence with depth, not deeper than the EM38 depth investigation, saying 2 meters. By eliminating the unlikely event that a huge conductive thin layer exists, we consider that a maximum of three homogeneous layers can been resolved, whatever the measurement procedure is. It is an inverse problem, and the precise subject of this paper.

2. The EM38: basics, field procedure, accurate drift correction

2.1 Basics

The Technical note written by McNeill (1980) provides the response of the apparatus in the presence of a layered media. In the present paper, we mainly consider a two horizontally (parallel to the surface) layered structure with an upper layer of conductivity σ_1 and thickness h, and a second layer of conductivity σ_2. In the VDM (Vertical Dipole Mode), the apparent conductivity (while the device is lying on the ground) is given by (*s* being the inter-coil spacing):

$$\sigma_a^V = \sigma_1[1 - R_V(z)] + \sigma_2 R_V(z) \quad \text{with} \quad R_V(z) = \frac{1}{\sqrt{4z^2+1}} \quad \text{where} \quad z = h/s$$

The HDM (Horizontal Dipole Mode) is given by:

$$\sigma_a^H = \sigma_1[1 - R_H(z)] + \sigma_2 R_H(z) \quad \text{with} \quad R_H(z) = \sqrt{4z^2+1} - 2z$$

Most of the time, both modes VDM and HDM are used together. This “pair” of data can also be substituted by using two different instruments, like in Sudduth et al. (2010) who use both EM38 from GEONICS and DUALEM-2S from DUALEM to characterize a clayey horizon.

An alternative field procedure consists in holding the apparatus at a given height Z above the ground to provide an additional measurement. Then the apparent conductivity integrates in a different way the conductivity with depth: the weight of the shallow depths (topsoil) is decreased while the greater depth (subsoil) contribution is higher. Then the apparent conductivity is given by (this for the vertical mode, the horizontal being straightforward):

$$\sigma_a^Z(T) = \sigma_1 \left[R_V\left(\frac{Z}{s}\right) - R_V\left(\frac{h+Z}{s}\right) \right] + \sigma_2 R_V\left(\frac{h+Z}{s}\right).$$

More generally, EM induction “soundings” can be performed with Slingram by two methods:

- Method 1: increase of the coil spacing; as far as GEONICS is concerned, one could join all or at least two of the devices EM38-MK2, EM31-SH, EM31, EM34, that gather the spacings: 0.5 m, 1 m, 2 m, 3.66 m, 10 m, 20 m, and 40 m and the use of both vertical and horizontal modes permits to collect 14 independent values. Such a method is used for instance by Triantafilis and Monteiro Santos (2009), by using EM38 and EM34 systems and the same authors in 2010 with an EM38 and an EM31. The “pair” of data VDM and HDM can be substituted in the same way to reach two different investigation depths by using two different instruments, like in Sudduth et al. (2010) who use both EM38 from GEONICS and DUALEM-2S from DUALEM to characterize a clayey horizon.
- Method 2: increase of the height of a single instrument above the ground, like in Hossain *et al.* (2010). The higher the instrument is, the deeper the investigation depth, but at the same time the S/N ratio is decaying due to the increasing remoteness.

2.2 Calibration: note on the classical scheme

The EM38 requires two main calibrations steps: the first devoted to the in-phase component (providing a signal depending on the susceptibility –not discussed here), and the second devoted to the compensation of the primary field phase error, which is discussed hereafter. The second step concerns the quadrature-phase signal, and actually consists in vanishing the drift value at one point. Following this, the drift may reach several mS/m in a few minutes or tens of minutes, and hence must definitely be taken into account and corrected for.

This usual calibration scheme is based on the following and is based first on a thin conductive layer response at a distance z underneath the instrument. This case leads to a couple of response in VDM and HDM that have the ratio:

$$\frac{\Phi_V}{\Phi_H} = \frac{4z}{(4z^2+1)^{3/2} - 2z(4z^2+1)} = \varphi(z).$$

The function $\varphi(z)$ is plotted on Figure 1.

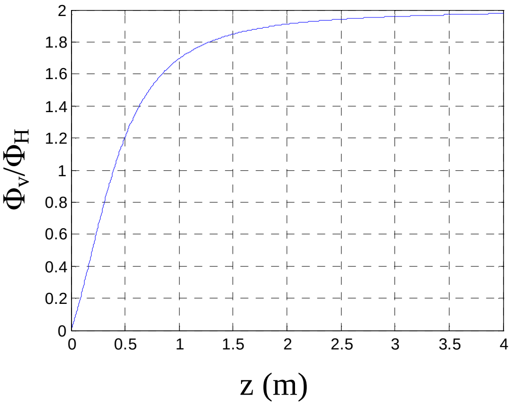


Figure 1. Ratio of Φ_V/Φ_H plotted against the distance z (m)

The ratio tends to 2 while z increases with 7% accuracy when z=1.5. This is the base of the calibration method (vanishing the offset drift) suggested by GEONICS in the EM38 manual: the ratio is adjusted to be 2 when the apparatus is put at 1.5 m height above the ground. The 7% error could appear not enough accurate, however this applies to a couple of measurements already relatively far from the ground. Precisely, the error is less than 1 mS/m in absolute if the conductivity observed at this height is less than 14 mS m^{-1} (7% of 14 mS m^{-1} =1 mS m^{-1}). This value would be the apparent conductivity we would observe at this height if the half-space had a homogeneous conductivity of 44 mS m^{-1}. In other words, this calibration procedure is accurate at the level of 1/44=2%, and generally it is even better because not only the very superficial layers contributes to the signal but the deeper ones too and even more (by integration), and also because the natural heterogeneities would make a higher accuracy requirement unrealistic. It is a fact that this matter of accuracy after calibration is rarely mentioned in the literature, this could be because these devices are more often used for qualitative featuring than accurate inversion.

If the EM38-MK2 is used, it involves also 50 cm coil spacing and we must consider that we have two instruments in one (even if the transmitter is common) and do the calibration separately for both spacings. The equivalent required height to calibrate is 1.5 m/2=75 cm, but of course the 1.5 m is even better and can be used at the same time than for the 1 m spacing.

2.3 Field procedure and accurate drift corrections

With the modern EM38, the data can be recorded by using an “auto”, walking mode, in which the measures are collected with a time rate of several readings per second. However, this introduces disturbances and fluctuations in the data (for instance because the height of the device above the ground is not strictly constant) and should be avoided if inversion of the data is planned. Then a regular grid or any kind of profile can be undertaken, by using any positioning system. In the following, we use in this study a regular grid obtained by gathering lines spaced by 5 meters. Also equally-spaced data in each line (called stations, as usual in geophysics) are collected with the same spatial sampling rate. The x-axis of the map matches the line number while the y-axis is relative to the stations. Profiles are parallel to the lines (y-axis) and are 50 m long.

The main difficulty to manage when accuracy better than 1 or 2 mS m^{-1} is required is relative to the drift. Although it has been strongly reduced in the 1-m spacing of the recent EM38-MK2, it is significant in the previous generation but also in the EM38-MK2 as far as the 0.5 m inter coil distance is concerned. This drift is purely instrumental, and can be due to some dilatation of the “chassis”, or to electronic drifts, and is mainly due to temperature effect, as previously mentioned.

In his already cited paper, Robinson *et al*. (2004) provided a study of the cause of the drift, and some means to reduce its effect. He reported the drift in terms of % of the measurement, but we prefer consider that it is an offset instead of a factor and hence we consider the drift as an additive effect (a shift). Although the drift is not very critical when observing high conductivities and when the need is semi-quantitative (for instance when used to map relative salinity), it becomes prohibitive when it is reaches the same order of magnitude than the expected signal, and this is frequent when the conductivity is low, saying less than 10 mS/m, and prevent any possibility of accurate inversion.

Several strategies can be used to reduce the effects of the drift;

- Posterior filtering basics on expected statistic to which the signal is forced (for instance, assuming that all the means of the different profiles should be equals). This procedure can by satisfying but misses the absolute values;
- Repeating calibration as soon as possible (for instance for each profile). However this is only efficient a short time after the calibration operation;
- Using cross-over profiles, and reduce the drift by analysing the cross-over discrepancy, from the beginning;
- Measuring it regularly, establish a curve by interpolation, and correct for this drift. This is the same method than the one used in gravity of magnetic (for instrumental of natural time variations).

According to us, the later is the most accurate method, and we describe below a detailed method which can be used in practice, based on the theory of the instrument.

Managing the drift with efficiency:

In any case, it is relevant to calibrate the instrument at the very beginning of the survey. Then, to estimate the drift, a first method consists in performing regular measurements in time, *at the same location*, and this permits to collect a set of data to be interpolated in time. This first method has a disadvantage. It is time consuming because it requires coming back regularly in time at the same location (typically each 15 min).

A second method we tested is much more efficient. It consists in calculating the drift at any location by using the factor 2 principles at 1.5 m height. The method begins with the computation of the drift suggested by GEONICS in the EM38 to calibrate the instrument, but goes further in the use of this calculation. First consider that the instrument is drifted (actually shifted!), and then we have:

$\frac{\sigma_V^a(1.5)}{\sigma_H^a(1.5)} \neq 2$ at 1.5 m height (in the following we drop the reference to this height). The offset C to be applied to the readings to get a factor 2 exactly is obtained by solving the equation: $\frac{\sigma_V^a + C}{\sigma_H^a + C} = 2$ from which we can derive C as $C = \sigma_V^a - 2\sigma_H^a$. Applying C to the readings corrects from the drift, and then the drift is simply:

$$D = -C = 2\sigma_H^a - \sigma_V^a.$$

It follows this practical method to correct from the drift:

- First make an initial calibration ;
- 1st drift measurement: instrument 1.5 m above the ground, “where you are”
- Making a set of measurement (5 to 20)
- 2nd drift measurement, “where you are”
- Making a set of measurement
- 3rd drift measurement, “where you are”
- ...
- ...
- Last drift measurement, “where you are”

No re-calibration has to be done (no adjustment of potentiometers), and the data are post-corrected from the drift by interpolation of the drift measurement at measured times.

In this paper, we reached an accuracy lying between 1 and 2 mS m^{-1}, by measuring the drift each 22 points. It would have been a little bit better to repeat each 5 or 10 points.

3. Inversion of the data

3.1 Short review on non-Bayesian methods

Several situations may arise:

1) No inversion is done, and only raw conductivity maps are proposed;
2) No inversion based on physical law is done, but some correlation between the apparent conductivity and the targeted parameter are established to convert the data into soil parameters. Domsch and Giebel (2004) use this method and for instance directly convert the apparent conductivity in texture features of the soil by using established correlations. Those methods are surely robust, but could miss the role of some "law of equivalence" and correlation between parameters;
3) Inversion is done, with the number of data less than the number of parameter of the model; it is the so-called "undetermined case" (Menke, 1989). In that case, some *a priori* information is necessary to perform the inversion. Within the EM38 community, this *a priori* is often taken as a Thikonov regularization which consists in including a certain level of smoothness of the model. In term of *a priori* covariance matrix, it is equivalent to a diagonal dominant. It is the way suggested by Deidda et al. (2003) and Hendrickx et al. (2002);
4) Inversion with the number of data being the same than the number of parameters (for instance two conductivities and one thickness to be retrieved from 3 apparent conductivities). It is named the "even-determined case". Hence an analytical inversion should be possible. However it can be shown that it is feasible only under some conditions, and we discuss further this possibility in brief;
5) Proper inversion where the number of data is higher than the number of parameter to be recovered: the "over determined case". Then least-square (with or without damping) is the most common way to manage that case.

Notice that a very general frame theory to encapsulate all the inversion methods is provided by the Bayesian approach, as shown by Tarantola and Valette (1982a and 1982b).

We discuss below point 4) and 5) since the other points have been widely developed in the literature, and we will only deal with the simple two homogeneous layer model (because it followed the example case we choose):

Model type 1: topsoil of conductivity σ_1 and thickness h, subsoil of conductivity σ_2 down to the limit if the investigation depth of the EM38 (saying about 2 m in practice). Three parameters are unknown: σ_1, σ_2 and h.

3.1.1 Analytical inversion with the classical EM38 (1 spacing s=1m)

To retrieve three parameters $\{\sigma_1, \sigma_2, h\}$, three measurements are required. With a classical EM38, it could be the two modes on the ground (VDM and HDM) plus a third measurement, for instance a measurement in the VDM with the instrument hold at a given height above the surface, for instance Z (=50 cm in our case), to gather an additional measurement with a larger depth investigation. The set of data leads to consider a system of three equations with three unknowns (with σ_a^V and σ_a^H are the data in VDM and HDM respectively (the apparatus on the ground) and σ_a^Z the apparent conductivity when the device is hold vertically at a height Z over the surface.

$$\begin{cases} \sigma_a^V = \sigma_1[1 - R_V(h)] + \sigma_2 R_V(h) = \sigma_1[1 - R_V] + \sigma_2 R_V \\ \sigma_a^H = \sigma_1[1 - R_H(h)] + \sigma_2 R_H(h) = \sigma_1[1 - R_H] + \sigma_2 R_H \\ \sigma_a^Z = \sigma_1[R_V(Z) - R_V(Z+h)] + \sigma_2 R_V(Z+h) = \sigma_1[R_v^0 - R_V^h] + \sigma_2 R_v^h \end{cases}$$

The third term of each line is just a simplification for the notation.

3.1.2 Analytical inversion with the EM38-MK2 (2 spacings s=1 m and s=50 cm)

For the EM38-MK2, it is natural to consider both modes with the 1 m spacing but then we suggest keeping only the vertical mode for the 50 cm spacing. The horizontal mode has a very superficial response. As it is difficult to really lay down the apparatus horizontally at the surface especially in the presence of grass, this is the noisiest measurements that can be done. We can thus ignore it to keep three values only to be analytically inverted. Notice that the direct calculation can be improved by including a thin air layer that would take into account the effective height of the coil centre (even different depending on the vertical or horizontal mode).

In that case, the system is: (the ~ hold for the 50 cm spacing).

$$\begin{cases} \sigma_a^V = \sigma_1[1 - R_V] + \sigma_2 R_V \\ \sigma_a^H = \sigma_1[1 - R_H] + \sigma_2 R_H \\ \sigma_a^{\tilde{V}} = \sigma_1[1 - R_{\tilde{V}}] + \sigma_2 R_{\tilde{V}} \quad \text{where} \quad R_{\tilde{V}} = \dfrac{1}{\sqrt{h^2+1}} \end{cases} .$$

Mathematically speaking theses systems can be solved as far as the correspondence between the observations and the parameters is exact. When solving it by linearly eliminating first σ_1 and σ_2 leads to single equation f(h)=0 which can be solved numerically (or even analytically). The situation described above is ideal, but in practice, it is frequent that the existence of a solution is not assured. The data are marred by errors and the system we try to solve (like the two given above for the two kinds of EM38) may have no solution at all. It is due to the fact that the image space of the application $\{\sigma_1, \sigma_2, h\} \mapsto \{\sigma_a^V, \sigma_a^H, \sigma_a^{\tilde{V}}\}$ is just a little part of $\Re^3$ and often the effective noisy measured triplets do not correspond to any original models in the parameter space. The case is identical to the one we meet when considering an electrical sounding in the two-layer case, for which it is not possible to draw a sounding curve crossing exactly the observed data, if these data are marred by some noise. This difficulty occurs because the sounding is supposed to be a very smooth and noisy data cannot be fitted. To better understand this limitation, imagine you know exactly two of the data, saying for instance σ_a^V and $\sigma_a^{\tilde{V}}$. We asked the following question: "knowing this data, what is the possible interval for σ_a^H?" Actually it often occurs that the measured value is not in the interval of the possible values, due to error, and then there is no solution to the system.

3.1.3 The case of two measurements to retrieve the three parameters of Model 1, when a third parameter is given by some other sources

Analytical resolution works in some special cases and if we only consider two equations with two unknowns, assuming the third parameter is known. It is the case if, for instance, an operator measures DV and DH modes with the instrumental lying on the ground. The situation is better than in the previous case because the latitude of solution is less restricted. Moreover, in these cases, some simple conditions of the existence or the solution can be derived and easily checked. If a high contrast applies to the current structure conductivities (saying >10), the sensitivity of the method to the layer having the lower conductivity one is weak and then it is often better to set this conductivity to a given value, or even to zero.

3.2 The least-square (LSQ) method and other relative methods

It is not our aim here to investigate the numerous variants of the least-square inversion scheme which can be used to manage the EM38 data inversion. As far as the least square method itself is concerned (whatever it is applied to), the paper by Tarantola and Valette (1982a) synthesizes and unifies several classical methods. When applying all methods to the inversion of EM38 data it is absolutely necessary to introduce a positivity constraint on both conductivities and thicknesses of the layered model, otherwise most of the algorithms may be unstable. The best way is to use the logarithm of the parameters instead of the parameters themselves, and this also takes into account that all the parameters are Jeffrey's parameter (see Tarantola, 2005 and 2006). Less conventional methods have not been studied enough in the literature, but probably will work well, like the Particle Swarm Optimization (PSO), see for instance Trelea (2003), or the Simulated Annealing method (Kirkpatrick et al. 1983). and surely the homotopy method as described by Jegen et al (2001) which is also used by Ghorbani et al. (2009) to invert Induced Polarization data.

In the frame of the Bayesian approach we are going to develop below, the least-square method appears as the research of the minimum of the Euclidian distance between the observed and calculated model, and hence is equivalent to the search for the maximum of multidimensional probability law the Bayesian method fully explores in the parameter space.

4. Bayesian methods

4.1 Principle of the method

The Bayesian approach consists in working with the probability density functions (pdf), or just "probability measures" when the probability laws cannot be normalized. Through the Bayesian theorem, the Bayesian method joins, gathers and crosses the knowledge we have before making any measurements (the *a priori* knowledge) and the new emergent knowledge provided by the measurement campaigns. The *a priori* includes not only some insight we have on the parameters but also the choice of the model itself, that is the two layers model we use here is a part of the *a priori* knowledge.

The Bayesian method has been widely discussed since the synthesis developed in Tarantola (2005). We use here an implementation similar to the one used by Ghorbani et al. (2007), where all the required concepts are detailed and then we drop here some necessary consideration which can be found in the cited paper. We just recall the basics.

Let $\vec{d}$ be the data and D the data space, $\vec{m}$ the model and $\vec{d} = G(\vec{m})$ the physical law linking these quantities. In the case of over determined inversion we have

$$M = \dim(\vec{m}) < \dim(\vec{d}) = D.$$

Let be $\mu(\vec{m})$ the "homogeneous probability measure" (see Tarantola 2005). Notice that if $\vec{m} = (m_1, m_2, ...m_{\dim(M)})$ are all Jeffrey's parameters, then we have

$\mu(\vec{m}) = \frac{1}{m_1}\frac{1}{m_2}....\frac{1}{m_M}$ (It is the case since conductivities and thicknesses are Jeffrey's parameters).

Notice that since we generally apply logarithm transformations to all Jeffrey's parameters, then it can be shown that $\mu\left(\log(m_k)\right) = 1, \forall k$, and this simplifies the computation by dropping this term.

In our model, all parameters are of Jeffrey type. The "homogeneous probability measures" (-previously called the "null information" (see Tarantola 2005)) are:

$$\left\{ \mu_1(\sigma_1) = \frac{C_1}{\sigma_1};\ \mu_2(\sigma_2) = \frac{C_2}{\sigma_2};\mu_3(h) = \frac{C_3}{h} \right. \quad ;$$

One chocking features of these probability measures is that they cannot be normalized. In practice, they are always involved in more complex expression of pdf that are normalizable and comes from the Shannon modern definition of informational entropy (see Tarantola and Valette, 1982a).

Then we systematically use the logarithms (see Ghorbani et al. (2007) to benefit from a more detailed discussion), so we made the following changes:

$\sigma_1^{\log} = \log(\sigma_1);\ \ \sigma_2^{\log} = \log(\sigma_2);\ \ h^{\log} = \log(h)$. It is suitable and just more convenient to take the logarithm in base 10.

Now let note $\phi(\vec{m})$ the *a priori* pdf for parameters. This pdf is logically speaking not the full *a priori* knowledge, but only the quantitative part of it. The density ϕ could be Gaussian, or anything we want. In our case, we use the combination (product) of a Gaussian pdf, with the indicator function of the interval we are exploring to find the parameters.

Let be for instance, the following *a priori* information: " $\sigma_1^{\log}$ could be close to 0.5 ± 0.3 " (we must translate into: $\sigma_1^{\log}$ follows a Gaussian distribution of mean 0.5 and standard deviation 0.3, that is σ_1 is supposed to be close to 3.13 with a 30% error), and we only pursue the value between 0 and 1. Then, then *a priori* pdf is given by:

$\phi(\sigma_1^{\log}) = C \cdot I(0,1) \cdot e^{-\frac{1}{2}\left(\frac{\sigma_1^{\log}-0.5}{0.3}\right)^2}$, where C is a constant of normalisation and I (0, 1) the index function valued 1 in the interval [0 , 1] and 0 outside.

The same applies to the other parameters and the full 3-variables *a priori* is just the product of the three.

As we show later on, the inclusion of a Gaussian to the bounded exploratory *a priori* domain permits to restrain the negative effects of the equivalence laws having hands in the determination of the parameters of the layered medium.

We also suppose that the data are Gaussian, having a covariance matrix C_{dd}

Then, the pdf of the parameters, which is also *the* solution of the inverse problem, is given by:

$$\mathrm{pdf}\,(\vec{m}) = \frac{\phi(\vec{m}) e^{-\frac{1}{2}\left[\vec{d}-G(\vec{m})\right]^T C_{dd}^{-1}\left[\vec{d}-G(\vec{m})\right]}}{\mu(\vec{m})}$$

It is the quantity we compute and plot in Bayesian inversion. In our case, thanks to the logarithm change of variable, we can drop the homogeneous probability measure (because it becomes constant), and also for the same reason, this pdf can be computed directly by a systematic exploration over a regular grid (3 dimensional) sweeping the parameters inside pre-defined intervals. So we can here fully explicit the computation with the following steps:

1) Define exploratory intervals and grids for $\sigma_1^{\log}$, $\sigma_2^{\log}$ and $h^{\log}$, for instance

Grid for $\sigma_1^{\log}$: from $\sigma_{1\min}^{\log}$ to $\sigma_{1\max}^{\log}$ in N_{σ_1} regularly spaced points

Idem for the other parameters, leading to the index function: $I\left(\left[\sigma_{1\min}^{\log}\ ,\ \sigma_{1\min}^{\log}\right];\left[\sigma_{2\min}^{\log}\ ,\ \sigma_{2\min}^{\log}\right];\left[h_{\min}^{\log}\ ,\ h_{\min}^{\log}\right]\right)$. Practically it implies that we shall only explore the parameter space within this 3-D box over $N_{\sigma_1} \times N_{\sigma_2} \times N_h$ points.

2) Define (or not) an *a priori* Gaussian (or another) law for the parameters. For instance, the following supposes only Gaussian *a priori* for $\sigma_1^{\log}$ and $h^{\log}$ but no additional law for $\sigma_2^{\log}$, (that is: the law is uniform in the relative interval) but Gaussian *a priori* for $\sigma_1^{\log}$ and $h^{\log}$:

$$A(\sigma_1^{\log},\sigma_2^{\log},h) = \exp\left[-\frac{1}{2}\left(\left(\frac{\sigma_1^{\log}-\overline{\sigma}_1^{\log}}{\delta\sigma_1^{\log}}\right)^2+\left(\frac{h^{\log}-\overline{h}^{\log}}{\delta h^{\log}}\right)^2\right)\right],$$ where δX names the standard error on the parameter X and where $\overline{X}$ is for the most probable value or mean. We drop here and often the normalization constant in factor of the pdf, because the normalization can be performed at the end of the process. This achieves the definition of our choice of *a priori* pdf, which is: $\phi = I \cdot A$.

3) The data supposed Gaussian distributed, the law relative to the experiment results is:

$$D(\sigma_1^{\log},\sigma_2^{\log},h) = \exp\left[-\frac{1}{2}\left(\left(\frac{\sigma_a^{V\,th}-\sigma_a^{V\,obs}}{err(\sigma_a^{V\,obs})}\right)^2+\left(\frac{\sigma_a^{H\,th}-\sigma_a^{H\,obs}}{err(\sigma_a^{H\,obs})}\right)^2+\left(\frac{\sigma_a^{Z\,th}-\sigma_a^{Z\,obs}}{err(\sigma_a^{Z\,obs})}\right)^2\right)\right]$$

in the case where an additional measurement has been added, for instance by holding the apparatus at a height Z, or:

$$D(\sigma_1^{\log},\sigma_2^{\log},h) =$$
$$\exp\left[-\frac{1}{2}\left(\left(\frac{\sigma_a^{V\,th}-\sigma_a^{V\,obs}}{err(\sigma_a^{V\,obs})}\right)^2+\left(\frac{\sigma_a^{H\,th}-\sigma_a^{V\,obs}}{err(\sigma_a^{H\,obs})}\right)^2+\left(\frac{\sigma_a^{\tilde{V}\,th}-\sigma_a^{\tilde{V}\,obs}}{err(\sigma_a^{\tilde{V}\,obs})}\right)^2+\left(\frac{\sigma_a^{\tilde{H}\,th}-\sigma_a^{\tilde{V}\,obs}}{err(\sigma_a^{\tilde{H}\,obs})}\right)^2\right)\right]$$

when both 1 m and 50 cm (noted with ~) has been measured with the EM38-MK2 for instance.

Finally the function to estimate is the 3-D pdf:

$P(\sigma_1^{\log},\sigma_2^{\log},h)=I(\sigma_1^{\log},\sigma_2^{\log},h)\cdot A(\sigma_1^{\log},\sigma_2^{\log},h)\cdot D(\sigma_1^{\log},\sigma_2^{\log},h)$, and even the homogeneous probability measure is taken into account because $P(\sigma_1^{\log},\sigma_2^{\log},h)$ is computed over a grid logarithmically defined by regular sampling of the log of the variables. Once it is computed one can normalize to get a true pdf just by:

$$p(\sigma_1^{\log},\sigma_2^{\log},h)=\frac{P(\sigma_1^{\log},\sigma_2^{\log},h)}{\iiint P(\sigma_1^{\log},\sigma_2^{\log},h)\,d\sigma_1^{\log}d\sigma_2^{\log}dh}$$

All the integrals above and below involve functions which are known on grids, then simple Riemann's sums can be performed to estimate them.

This function is the solution of the inverse problem: it allows calculating the probability for a set of parameter belonging to a given interval. It is:

$$\text{prob}(\sigma_1^{\log}\in\Gamma_{\sigma_1},\sigma_2^{\log}\in\Gamma_{\sigma_2},h\in\Gamma_h)=\int\limits_{\Gamma_{\sigma_1}}\int\limits_{\Gamma_{\sigma_2}}\int\limits_{\Gamma_h}P(\sigma_1^{\log},\sigma_2^{\log},h)d\sigma_1^{\log}d\sigma_2^{\log}dh$$

By the way, CPU/memory questioning aspect is necessary. The obtained function is 3-D. A grid saying of $100\times100\times100=10^6$ points is to be managed by the computer. Although it is still moderate, it would rapidly impossible to perform the calculation for bigger grids. Then two questions arise: first, is the exploratory domain large enough (will it contain the solution?) and second, is the grid thin enough to provide a good representation of the sampled pdf? There is a risk of aliasing or even missing the main features of the law if the grid is too coarse with respect to the sampled function. In the case when higher dimension problem must be tackled, it is useful to use special integration algorithms like the so-called "metropolitan" scheme (see Mosegaard and Tarantola, 1995).

4) How to utilize the solution and what representation for it?

The obtained pdf $P(\sigma_1^{\log},\sigma_2^{\log},h)$ is a function of three variables and can be represented by using 3-D plot. This kind of plot is useful for pure visual interpretation (see for instance Ghorbani 2007) but hardly usable to provide quantitative results. Moreover, the geophysicist is generally asked to provide some single value for each parameter, with the corresponding errors.

Hence it is relevant to plot the 2-D marginal laws, and, by cascading, the 1-D marginal laws, and finally the means and the relative deviation.

Here, the first step of marginal probability yields 3 laws of two parameters. Precisely:

$$\begin{cases} p_{\sigma_1^{\log}\sigma_2^{\log}}(\sigma_1^{\log},\sigma_2^{\log}) = \displaystyle\int_{h_{\min}^{\log}}^{h_{\max}^{\log}} p(\sigma_1^{\log},\sigma_2^{\log},h)dh \\ p_{\sigma_1^{\log}h}(\sigma_1^{\log},h) = \displaystyle\int_{\sigma_{2\min}^{\log}}^{\sigma_{2\max}^{\log}} p(\sigma_1^{\log},\sigma_2^{\log},h)d\sigma_2^{\log} \\ p_{h,\sigma_2^{\log}}(h,\sigma_2^{\log}) = \displaystyle\int_{\sigma_{1\min}^{\log}}^{\sigma_{1\min}^{\log}} p(\sigma_1^{\log},\sigma_2^{\log},h)d\sigma_1^{\log} \end{cases}$$

Then the law of one or the other parameter is given by an integral of the form:

$p_\alpha(\alpha) = \int p_{\alpha\beta}(\alpha,\beta)d\alpha\beta$ for any of the above pair.

Finally, one can compute the mean and centred variance from the law, with:

$$\overline{\alpha} = \int \alpha p_\alpha(\alpha)d\alpha; \quad \mathrm{var}(\alpha) = \int (\alpha - \overline{\alpha})^2 p_\alpha(\alpha)d\alpha$$

At this stage, it is easy to plot map of the inverted parameters if we have maps of apparent conductivity, and this mean is expected to be close to the least-square solution.

However, it is different from the least-square solution. Just consider the elementary LSQ solution, without any *a priori* or neither damping nor regularization parameter. It corresponds to the parameter set where the maximum of the function D given above is reached (the minimum of the exponent). The fundamental difference is that a parameter retrieved from this LSQ solution does not involve any integration over the other parameters. In the case of Gaussian laws, and more generally speaking symmetric PDF, it makes no difference, because those integrals are centred on the mean (even if the physical law involved is non linear). In any other cases, the Bayesian solution is preferable to the LSQ solution.

Moreover, the Bayesian solution preserves an interpretation in terms of information, and provides probabilities to characterize the parameters. Furthermore it facilitates the analysis of the equivalence laws by plotting the trade-off between the parameters.

The Bayesian approach also provides a powerful tool to analyse the equivalence problem that arises in some geophysical problems. Consider for instance the following problem: let assume a conductive topsoil of few decimetres thick and very resistive subsoil. Then we may write the following equivalence law:

$$\sigma_1\left(1 - R_V(h)\right) \equiv \sigma_1'\left(1 - R_V(h')\right) = \mathrm{const.}$$

That is, the doublet $\{\sigma_1, h\}$ will lead to the same apparent conductivities than $\{\sigma_1', h'\}$ specially while $\sigma_1 \to \infty$ and $h \to 0$ respecting the condition $\sigma_1\left(1 - R_V(h)\right) = \mathrm{const.}$

In a 2-D diagram with this parameter as coordinates, the equivalence law is clearly revealed. This Bayesian solution also leads to additional knowledge about the possible behavior of inversion scheme itself, and on the importance to set suitable *a priori* information to be included in. First notice that a classical least-square scheme solution can be at any location in the “valley” representing the valuable solution, depending on the initial point. A Tikhonov-like inversion will stabilize the solution around an *a priori* given set, if for instance a term like $(h-\overline{h})^2+(\sigma_1-\overline{\sigma}_1)^2$ is added to the current sum of squared errors, and surely is a improvement if the simple LS method, but may miss some other possibilities. ($\overline{h}$ and $\overline{\sigma}_1$ play the role of attractors for the solution).

While considering the mean of the pdf, the effect of the boundary of the exploration window will affect this mean dramatically, because –and it is mathematically true- it takes into account the possibility of peculiar values when $\sigma_1 \to \infty$ and simultaneously $h \to 0$. Those must be eliminated by applying physical and geological knowledge, that is, mathematically, by including a well-shaped *a priori* law into the inversion process.

5. References

Abdu, H., Robinson, D.A., and Jones, S.B., 2007. Comparing bulk soil electrical conductivity determination using the DUALEM-1S and EM38-DD electromagnetic induction instruments. Soil Sci. Soc. Am. J. 71:189-196. doi:10.2136/sssaj2005.0394

Brevik, E.C., Fenton, T.E., Lazari, A., 2006. Soil electrical conductivity as a function of soil water content and implications for soil mapping. Precision Agriculture 7, 393–404.

Cockx, L., Van Meirvenne, M., and De Vos, B., 2007. Using the EM38DD soil sensor to delineate clay lenses in a sandy forest soil. Soil Science Society of America Journal 71, 1314–1322.

Corwin, D.L., and Lesch, S.M., 2005. Apparent soil electrical conductivity measurements in agriculture. Computers and Electronics in Agriculture 46, 11–43.

Deidda, G.P., Bonomi, E., and Manzi, C., 2003. Inversion of electrical conductivity data with Tikhonov regularization approach: some considerations. Annals of geophysics 46, 549-558.

Domsch, H., and Giebel, A., 2004. Estimation of soil textural features from soil electrical conductivity recorded using the EM38. Precision Agriculture 5, 389–409. DOI: 10.1023/B:PRAG.0000040807.18932.80

Doolittle, J.A., Sudduth, K.A., Kitchen, N.R., and Indorante, S.J., 1994. Estimating depths to claypans using electromagnetic induction methods. Journal of Soil and Water Conservation 49, 572–575.

Ghorbani,A., Camerlynck,C., Florsch,N., 2009. CR1Dinv: A Matlab program to invert 1D spectral induced polarization data for the Cole–Cole model including Electromagnetic effects. Computers and Geosciences 35, 255–266. doi: 10.1016/j.cageo.2008.06.001.

Ghorbani,A., Camerlynck,C., Florsch,N., Cosenza, P., and Revil, A., 2007. Bayesian inference of the Cole–Cole parameters from time- and frequency-domain induced polarization. Geophysical Prospecting 55, 589–605

Hanson, B.R., Kaita, K., 1997. Response of electromagnetic conductivity meter to soil salinity and soil water content. Journal of Irrigation and Drainage Engineering 123, 141–143.

Hendrickx, J.M.H., Borchers, B., Corwin, D.L., Lesch, S.M., Hilgendorf, A.C., and Schlue, J., 2002. Inversion of Soil Conductivity Profiles from Electromagnetic Induction Measurements: Theory and Experimental Verification. Soil Sci. Soc. Am. J. 66, 673–685.

Hezarjaribi, A., Sourell, H., 2007. Feasibility study of monitoring the total available water content using non-invasive electromagnetic induction-based and electrode-based soil electrical conductivity measurements. Irrigation and Drainage 56, 53–65

Hossain, M.B., Lamb, D.W., Lockwood, P.V., and Frazier, P., 2010. EM38 for volumetric soil water content estimation in the root-zone of deep vertosol soils. Computers and Electronics in Agriculture 74, 100–109.

Jegen, M.D., Everett, M.E., Schultz, A., 2001. Using homotopy to invert geophysical data. Geophysics 66, 1749–1760. doi:10.1190/1.1487117

Kachanoski, R.G., De Jong, E., Van Wesenbeeck, I.J., 1990. Field scale patterns of soil water storage from non-contacting measurements of bulk electrical conductivity. Canadian Journal of Soil Science 70, 537–541.

Khakural, B.R., Robert, P.C., Hugins, D.R., 1998. Use of non-contacting electromagnetic inductive method for estimating soil moisture across a landscape. Communications in Soil Science and Plant Analysis 29, 2055–2065.

Kirkpatrick, S., Gelatt, C.D., and Vecchi, M.P., 1983. Optimization by Simulated Annealing, Science. New Series 220 (4598): 671–680. doi:10.1126/science.220.4598.671. ISSN 00368075. PMID 17813860. http://www.jstor.org/stable/1690046.

Kitchen, N.R., Sudduth, K.A., and Drummond, S.T., 1996. Mapping of sand deposition from 1993 Midwest floods with electromagnetic induction measurements. Journal of Soil and Water Conservation 51, 336–340.

Kitchen, N.R., Sudduth, K.A., and Drummond, S.T., 1999. Soil electrical conductivity as a crop productivity measure for claypan soils. Journal of Production Agriculture 12, 607–617.

Kitchen, N.R., Sudduth, K.A., Myers, D.B., Massey, R.E., Sadler, E.J., Lerch, R.N., Hummel, J.W., and Palm, H.L., 2005. Development of a conservation-oriented precision agriculture system: Crop production assessment and plan implementation. Journal of Soil and Water Conservation 60, 421–430.

Lesch, S.M., Strauss, D.J., and Rhoades, J.D., 1995. Spatial prediction of soil salinity using electromagnetic induction techniques: II. An efficient spatial sampling algorithm suitable for multiple linear regression model identification and estimation. Water Resources Research 31, 87–398.

Lund, E.D., Christy, C.D., and Drummond, P.E., 1999. Practical applications of soil electrical conductivity mapping. In: Precision Agriculture ’99, Proc. 2nd European Conf. on Precision Agriculture, Stafford, J.V. (ed.), Sheffield Academic Press Ltd., Sheffield, UK, 771–779.

McNeill, J.D., 1980. Electromagnetic terrain conductivity measurement at low induction numbers. Technical Note TN-6 downloadable at http://www.geonics.com/pdfs/technicalnotes/tn6.pdf

McNeill, J.D., 1992. Rapid, accurate mapping of soil salinity by electromagnetic ground conductivity meters in Advances in Measurement of Soil Physical Properties: Bringing Theory Into Practice, Spec. Pub. 30, Soil Science Society of America, Madison, Wisconsin 209–229.

Menke, W., 1989. Geophysical data analysis: Discrete inverse theory, Academic Press, San Diego.

Mosegaard, K., and Tarantola, A., 1995. Monte Carlo Sampling of Solutions to Inverse problems. Journal of Geophysical Research 10 12,431-12,447.

Mueller, T.G., Hartsock, N.J., Stombaugh, T.S., Shearer, S.A., Cornelius, P.L., and Barnhisel, R.I., 2003. Soil electrical conductivity map variability in limestone soils overlain by loess. Agronomy Journal. 95, 496–507.

Myers, D.B., Kitchen, N.R., Sudduth, K.A., Sharp, R.E., and Miles, R.J., 2007. Soybean root distribution related to claypan soil properties and apparent soil electrical conductivity. Crop Science 47, 1498–1509.

Rhoades, J.D., Manteghi, N.A., Shrouse, P.J., and Alves, W.J., 1989. Soil electrical conductivity and soil salinity: New formulations and calibrations. Soil Science Society of America Journal 53, 433–439.

Robinson, D.A., Lebron, I., Lesch, S.M., and Shouse, P., 2004. Minimizing drift in Electrical Conductivity Measurements in High Temparture Environments using the EM-38. Soil Science Society of America Journal 68, 339-345.

Saey, T., Simpson, D., Vermeersch, H., Cockx, L., and Van Meirvenne, M., 2009. Comparing the EM38DD and DUALEM-21S sensors for depth-to-clay mapping. Soil Science Society of America Journal 73, 7–12.

Saey, T., Simpson, D., Vitharana, U.W.A., Vermeersch, H., Vermang, J., and Van Meirvenne, M., 2008. Reconstructing the paleotopography between the loess cover with the aid of an electromagnetic induction sensor. Catena 74, 58–64.

Sherlock, M.D., McDonnell, J.J., 2003. A new tool for hillslope hydrologists: spatially distributed groundwater level and soil water content measured using electromagnetic induction. Hydrological Process 17, 1965–1977.

Sudduth, K.A., Drummond, S.T., and Kitchen, N.R., 2001. Accuracy issues in electromagnetic induction sensing of soil electrical conductivity for precision agriculture. Computers and Electronics in Agriculture 31, 239–264.

Sudduth, K.A., Kitchen, N.R., Myers, D.B., and Drummond, S.T., 2010. Mapping Depth to Argillic Soil Horizons Using Apparent Electrical Conductivity. Journal of Environmental and Engineering Geophysics 15, 135–146.

Tarantola, A., 2005. Inverse problem theory and methods for model parameter estimation. Society for Industrial and Applied Mathematics, http://www.siam.org/.

Tarantola, A., 2006. Elements for Physics - Quantities, Qualities, and Instrinsic Theories. Albert Tarantola, Springer.

Tarantola, A., Valette, B., 1982a. Generalized non linear inverse problem solved using the least square criterion. Reviews of Geophysics and Space Physics 20, 219–232.

Tarantola, A., Valette, B., 1982b. Inverse problems—quest for information. Journal of Geophysics 50, 159–170.

Trelea, I.V., 2003. The particle swarm optimization algorithm: convergence analysis and parameter selection. Information Processing Letters 85, 317–325

Triantafilis, J., and Monteiro Santos, F.A., 2009. 2-Dimensional soil and vadose-zone representation using an EM38 and EM34 and a laterally constrained inversion model. Soil Research 47, 809–820.

Williams, B.G., and Baker, G.C., 1982. An electromagnetic induction technique for reconnaissance surveys of soil salinity hazards. Australian Journal of Soil Research 20, 107–118.

Annexe 6. Application de l'inversion Bayésienne à Potshini

1. Raw data from EM38-MK2 in June 2010

A map of 100 mX150 m has been acquired with an EM38-MK2, with a grid mesh of 5 m by 5m in each direction. The data, corrected from drifts are shown on Figure 1.

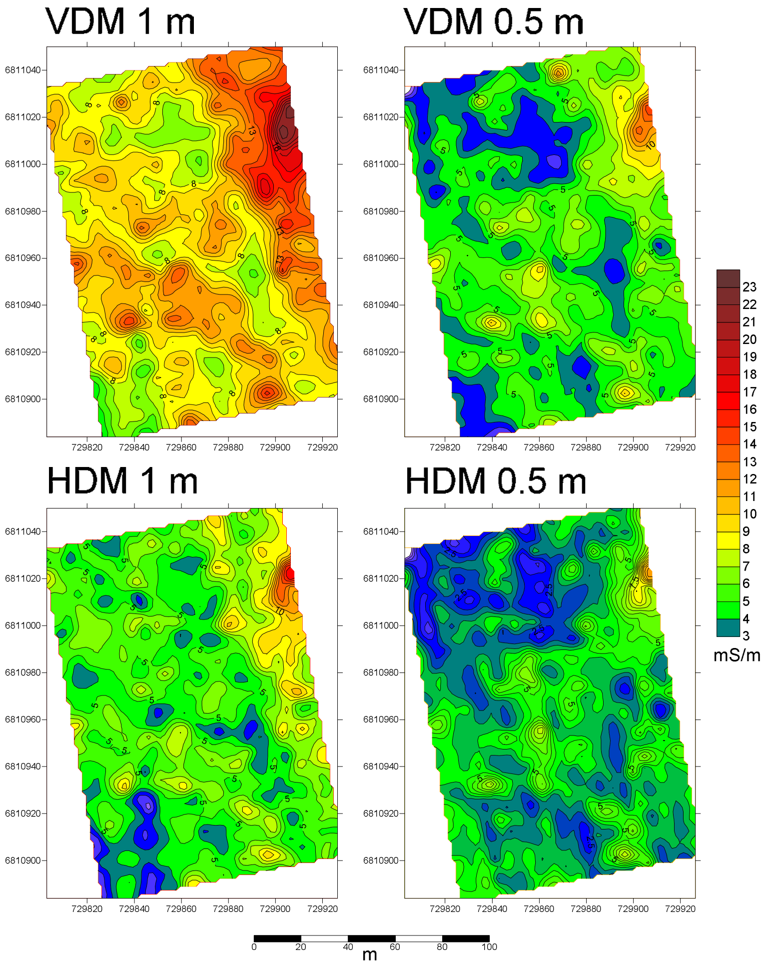


Figure 1. Raw EM38-MK2 data in June 2010 in both VDM and HDM (vertical and horizontal dipole modes) with spacings 50 cm and 1m. Coordinates are in UTM.

Before starting the inversion, it is useful to choose a model to be used, as a part of the *a priori* information that is available. First, the main feature of the soil can be inferred from just comparing the two VDM maps: the 1 m spacing data is much more conductive than the 50 cm one. Associated with field observation, this means that within the first meter, it is likely that we have a resistive layer over a conductive one.

The gully section provides an opportunity to make measurements and samplings on its wall, but limiting the depth due to security reasons. The amount of clay has been derived from samples taken each 5 cm on a vertical log (the size definition of clays is used here: particles less than 2 micrometers). The resistivity is measured by using a little pole-pole array (AM=3 cm), also on the face of the gully. Moreover, a Vertical Electrical Sounding (VES) has been made just apart from the ravine. The corresponding data are gathered on Figure 2. They all confirm the 2-layer simple horizontal structure of the ground and shows that it is valid to perform further inversion by assuming such a simple model involving a non-conductive layer covering a more clayey conductive layer. This soil at Potshini has been classified as a luvisol by soil scientists. The thickness of the topsoil in the gully section lies around 40 cm, but variability over the area does exist, and the general range is between 30 cm and 80 cm.

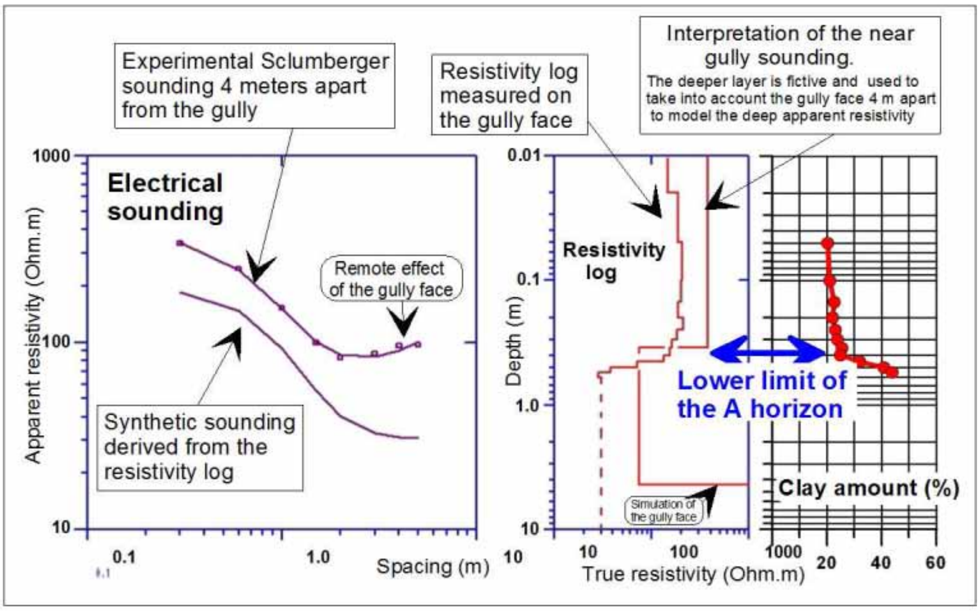


Figure 2. Correspondence between electrical sounding, resistivity values and clay amount on a gully bank wall in the studied grassland.

2. Bayesian inversion

From the information of Appendix 5, the *a priori* information can be set. It combines an exploration window and a light attractor to prevent for the mean to be found too high due to the equivalence problem.

Precisely, this *a priori* information is chosen here as:

$$\text{prior} = \mathrm{I}\left(1 \le \sigma_1 \le 10\right) \cdot \mathrm{I}(5 \le \sigma_2 \le 50) \cdot \mathrm{I}(0.3 \le h \le 1) \cdot e^{-0.5h^2}$$

where I are the index function (=0 or =1 depending if the value is within the given interval or not).

The a priori standard deviations of $\left(\sigma_a^V(s = 1m); \sigma_a^V(s = 50cm); \sigma_a^H(s = 1m); \sigma_a^H(s = 50cm)\right)$ are: (2 , 2 , 3 , 5). The error is supposed higher for the 50 cm spacing due to a higher drift, and also because it is more difficult to plate the instrument on the ground for this scale. An example of inversion results is given on Figure 3.

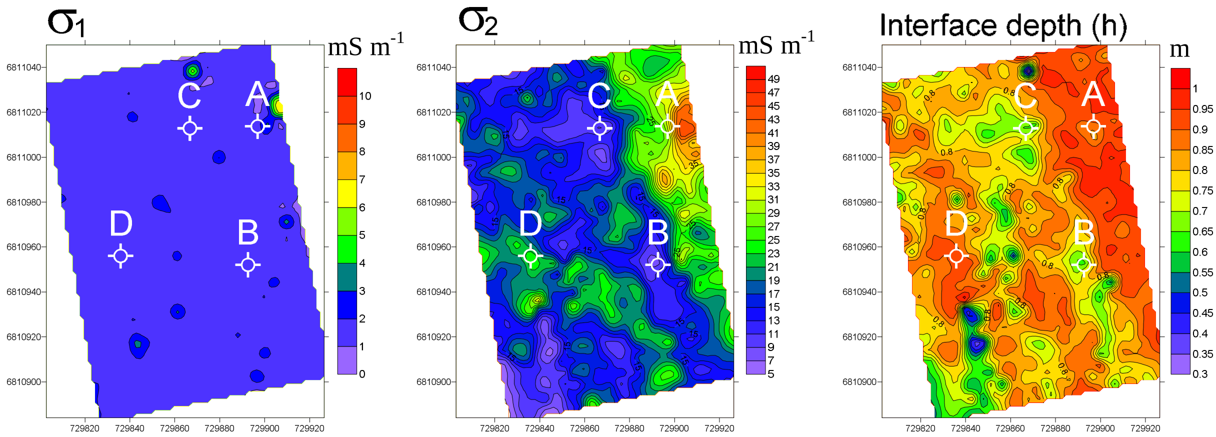


Figure 3. Results of the Bayesian inversion in June 2010. Points A, B, C and D are relative to the position of validation pit logs.

3. Validation of the inversion

Four shallow pits were available on the area (A, B, C, D), that permits comparison with the “field reality”.

3.1 Resistivity logs

In these pits, we did resistivity logs by using a pole-pole along the wall of the pit.
The resistivity diagraphies are given on Figure 4.

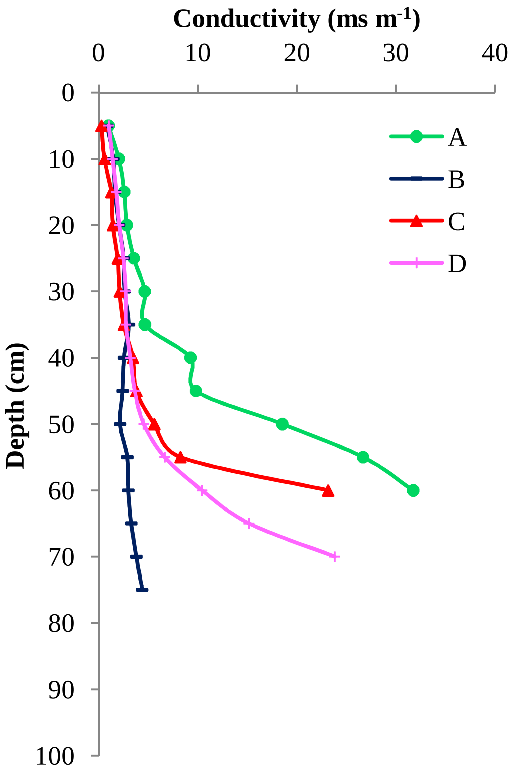


Figure 4. Conductivity log in four soil profiles in June 2010.

3.2 Methylene blue test method

In order to validate the depth of the interface determined from EC measured by the EM38-MK2 in the inversion process of the data, the methylene blue spot method is an easy and quick solution (Yukselen and Kaya 2008). This method gives information on clay properties (Hang and Brindley 1970) and can allow calculating for example cation exchange capacity (Kahr and Madsen 1995) or specific surface area (Santamarina et al. 2002, Yukselen and Kaya 2006) which should directly influence EC. By using this method, we will be able to estimate clay properties of soils at different depth and we should observe a similar transition that was calculated by the inversion procedure.

Methylene blue (MB) molecule is a cationic dye, $C_{16}H_{18}N_3S^+$ which can adsorb onto negatively charged clay surfaces (Yuskelen and Kaya 2008). Its dimension is 17 Å * 7.6 Å * 3.25 Å and the surface area covered by one molecule is approximately 130 $Å^2$ (Santamarina et al. 2002). By determining the quantity of methylene blue molecules that can be fixed onto clay surface of a specific soil, we can then determine clay properties of this soil. This easy applicable method is often used in geotechnical and construction work to estimate the resistance of clay to water (swelling of clay).

The method used in this study was as follow: soil samples were air dried and sieved at 4 mm. We mixed 30 g of soil fraction 0-4 mm with 200 ml of dionized water. This soil suspension was continually mixed by magnetic stirrer during the experiment. Methylene blue solution was prepared by mixing 5 g of dry power of MB with 500 ml of dionized water. The concentration of this solution was 10 g l^{-1}. Then MB solution was added into the soil suspension with 5 ml increment. A small drop was removed from the suspension one minute after each 5 ml addition of MB and placed onto filter paper. A circle appears onto the filter paper with a dark blue center composed by soil aggregates. If the unabsorbed MB forms a blue halo around the soil aggregate spot, then confirmation test is needed: drops are removed from the suspension every minutes during 5 minutes (without addition of MB); If the blue halo becomes permanent (after 5 drops), it means that MB has replaced cations in the double layer and coated the entire surface. If the blue halo disappeared during the confirmation test, then we carry on adding MB solution to the suspension.

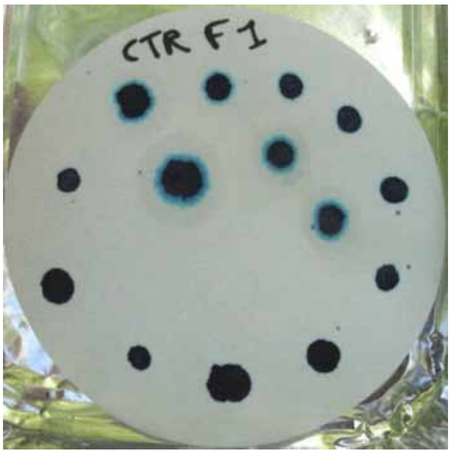


Figure 5. Methylene blue spot test on one soil sample and example of permanent blue halo after five confirmation tests.

The volume of MB necessary to replace all cations on clay surface globally increased with depths for the six studied profiles (Fig. 2). The increase of MB volume below the depth 40 cm for most of the profiles indicates that specific surface area of clay and CEC increased below 40 cm.

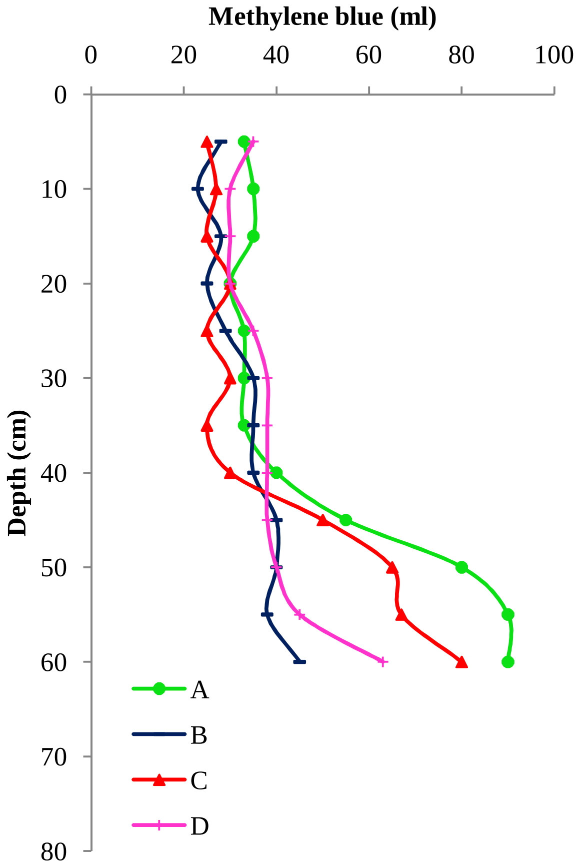


Figure 6. Methylene blue spot test results on soil samples of four soil profiles.

We observe that the conductivity and the clay content as revealed by the MB method are fully coherent, and this is not surprising since we consider that the clays are at the origin of the high conductivity values on this field. For example, the inflexion transition between the topsoil (A horizon in terms of soil science) and the subsoil (Bt layer) lies around 50 cm for the MB results and the conductivity log. However, close to this location, the inverted interface depth is given at 0.76 cm (Fig. 3). To better understand why this results seems to differ, let us consider the two-by-two marginal pdf. On Figure 7a is given a zoom of the (σ_2, h) pdf. It illustrates very clearly the equivalence (or trade-off) between these two variables. The lower admissible value for (σ_2, h) is $\left(10^{1.4} \square 25, 10^{-0.6} \square 0.6\right)$. If we remember that the Slingram tends to fetch the conductor, this can be considered as satisfying. Before debating deeper on the meaning of such a bias, we show on Figure 7b and 7c the pdf of the two other couples (σ_1, h) and (σ_1, σ_2) respectively.

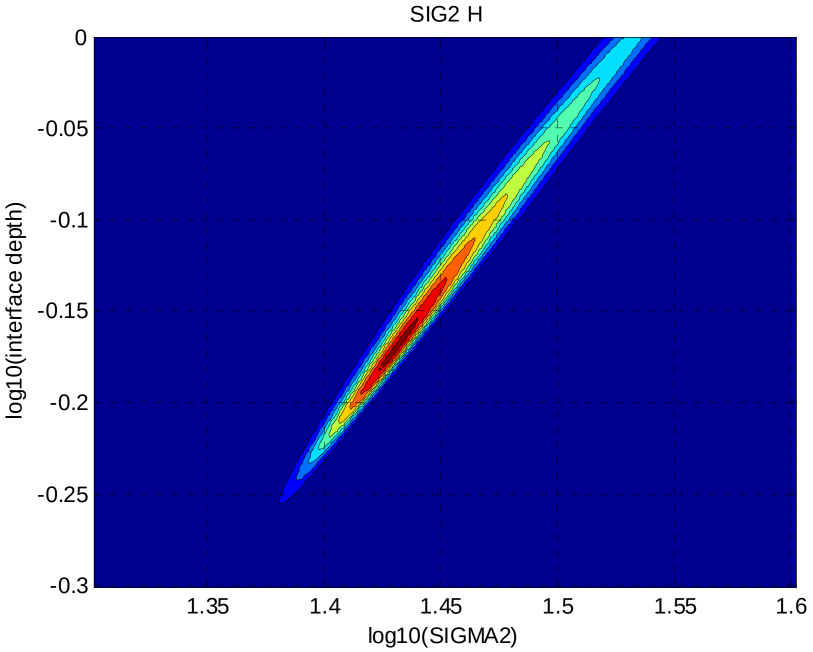


Figure 7a. Marginal pdf of (σ_2, h)

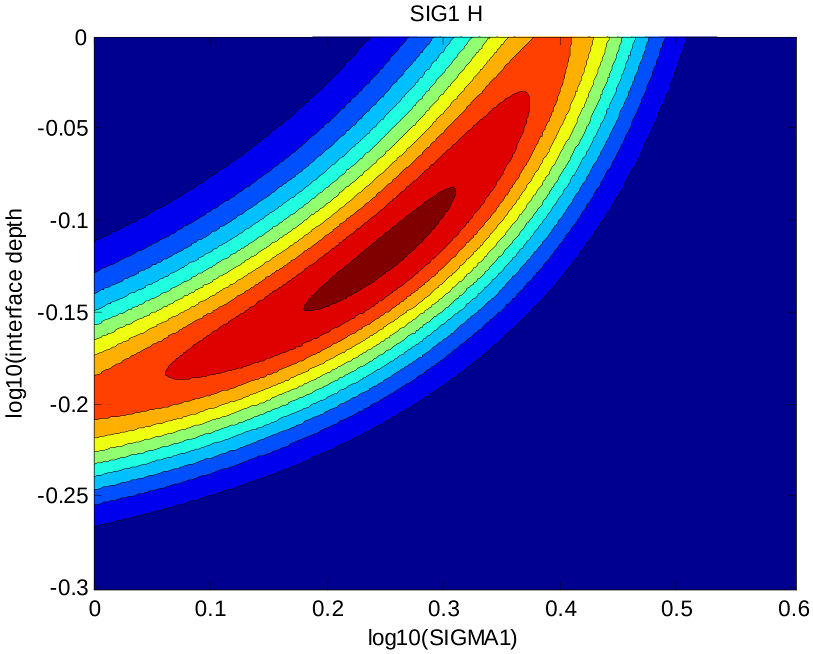


Figure 7b. Marginal pdf of (σ_1, h)

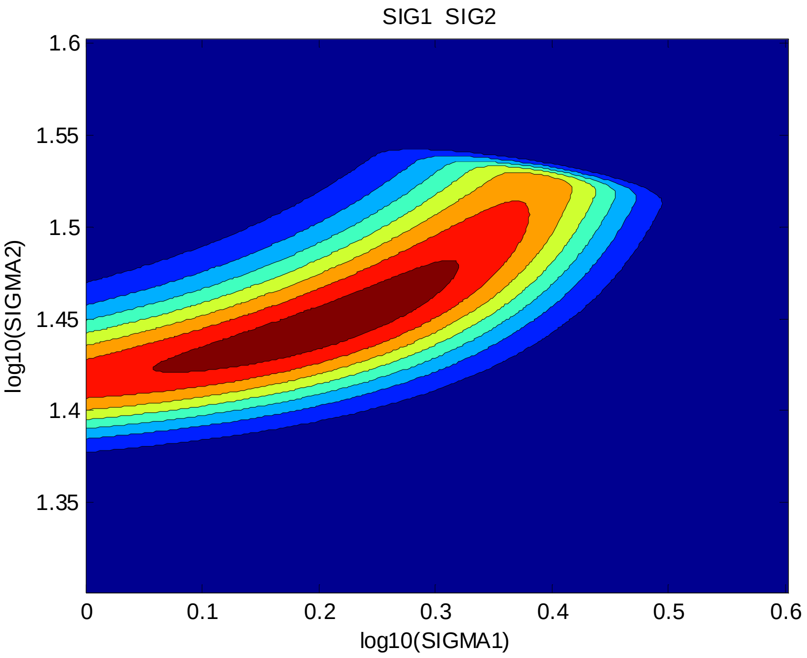


Figure 7c. Marginal pdf of (σ_1, σ_2)

On figure 7c we observe the peculiar shape of the upper right end of the pdf. It is the consequence of the *a priori* window (justified *a priori* knowledge) we embedded in the inversion, and particularly the set boundaries that correspond on the window limits as seen on Figure 7b.

3.3 Inversion bias

Tarantola and Valette in 1982 clearly state that the pdf "is THE solution of the inverse problem". They want to emphasize that, in the process of propagating the field experimental data through the physical law (including by the way the *a priori* information (or inversely), the Bayesian solution consists in the whole information that can be retrieved from the whole gathering of information. Actually, for practical purpose it is useful to provide only ONE value for the final parameter, and to do that the mathematical path consists in calculating the mean value of the parameter by computing the ultimate one-variable marginal probability density.

This bias is definitely inherent to the inverse problem. The LSQ method, assuming an attractor (that is: damping method or Marquardt-Levenberg algorithm) or special algorithms all includes at least the bias of the algorithm in own, but the bias itself is generally not easy to discuss within the information theory frame.

4. References

Yukselen, Y. and Kaya, A., 2008. Suitability of the methylene blue test for surface area, cation exchange capacity and swell potential determination of clayey soils. Engineering Geology, 102: 38-45.

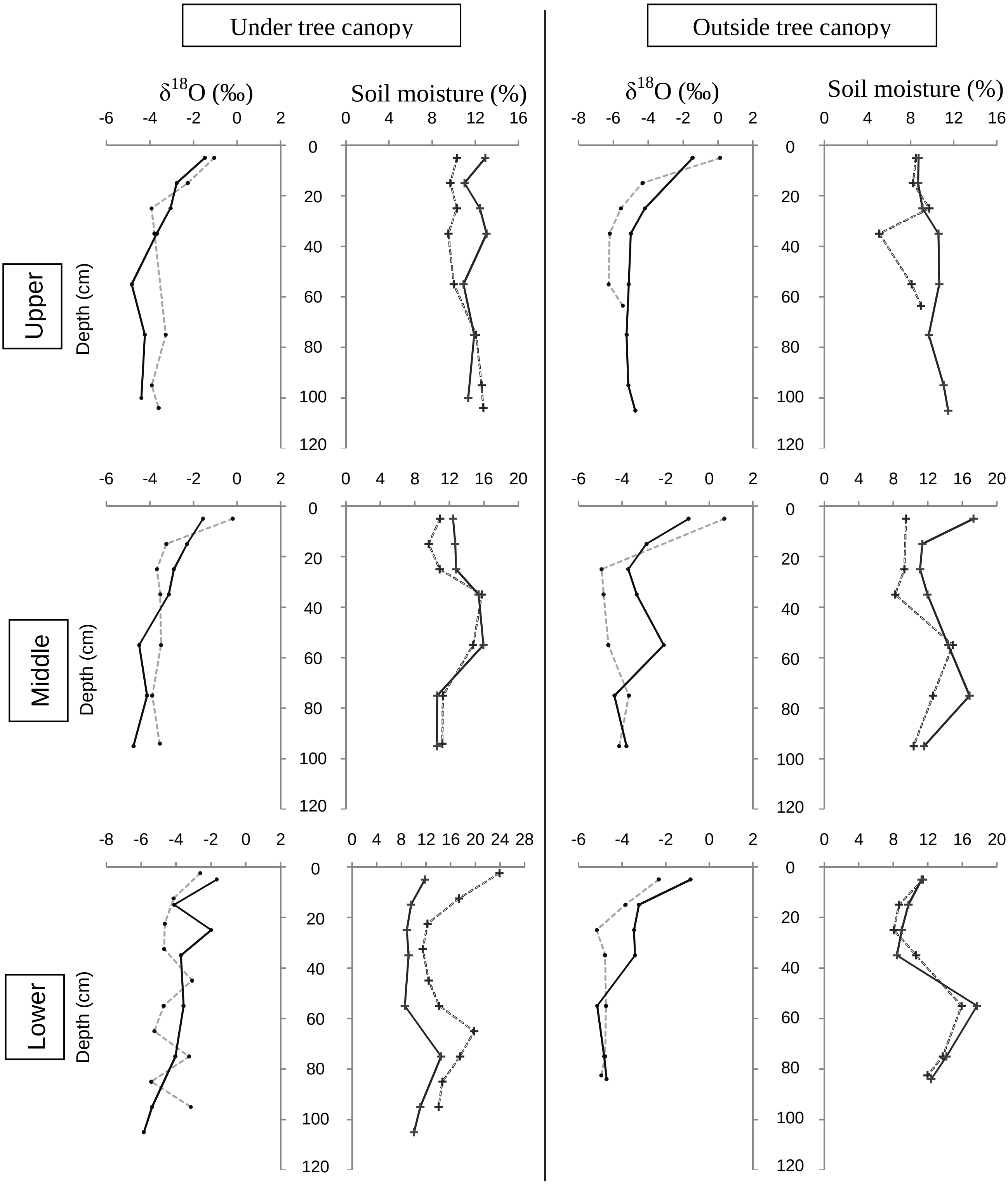
Hang, P.T. and Brindley, G.W., 1970. Methylene blue absorption by clay minerals. Determination of surface areas and cation exchange capacities (clay-organic studies XVIII). Clays and Clays minerals, 18: 203-212.

Kahr, G. and Madsen, F.T., 1995. Determination of the cation exchange capacity and the surface area of bentonite, illite and kaolinite by methylene blue adsorption. Applied Clay Science, 9: 327-336.

Santamarina, J.C., Klein, K.A., Wang, Y.H. and Prencke, E., 2002. Specific surface: determination and relevance. Canadian Geotechnical Journal, 39: 233-241.

Tarantola, A., Valette, B., 1982. Inverse problems — quest for information. Journal of Geophysics, 50, 159–170.

Annexe 7. Résultats isotopiques de six profils de sol supplémentaires



δ18O (‰) and soil moisture (%) values for extra soil profiles sampled under acacias canopy and outside canopy at the three zones in the catena (Upper, middle and lower part) in September 2009 (dotted lines) and in February 2010 (solid lines).

Annexe 8. Genres et espèces de la strate herbacée observés à Potshini

Genres et espèces de certaines plantes observées sur le pâturage de Potshini en 2009.

Asclepias gibba
Becium oboratum
Berkheya setifera
Centella asiatica
Centella coriacea
Chamaecrista sp.
Conyza sp.
Corchorus confusus
Corchorus junodii
Cyanotis speciosa
Cyperus sphaerocephalus
Diclis reptans sp.
Eriosema salignum
Gerbera sp.
Helichrysum rugulosum
Helicrysum sp.
Hermannia sp.
Hibiscus pedunculatus
Hirpicium sp.
Hypochaeris sp.
Hypoxis sp.
Ipomoea sp.
Lactuca sp.
Lantana rugosa
Ledebouria floribounda
Leonotis dysophylla
Leonotis leonurus
Leonotis microphylla
Leonotis nepetifolia
Momordica balsamina
Monopsis decipiens
Oxalis obliquifolia
Pelargonium luridum
Pentanisia angustifolia
Polygala sp.
Ranunculus multifidus
Richardia brasiliensis
Scabiosa columbaria
Schkuhria pinnata
Sebaea grandis
Senecio inaequidens
Senecio scaposus
Sida dregei
Solanum retroflexum
Thesium costatum
Thunbergia sp.
Verbenaceae sp.
Vernonia natalensis
Vigna sp.
Wahlenbergia sp.
Zornia linearis
Zornia capensis

Genres et espèces de la famille des Poacées (Graminées) observées sur le pâturage de Potshini en 2009.

Aristida junciformis
Aristida canescens
Aristida diffusa
Brachiaria eruciformis
Brachiaria serrata
Chloris virgata
Cymbopogon plurinodis
Cymbopogon excavatus
Cynodon dactylon
Digitaria longiflora
Eleusine coracana
Eragrostis curvula
Eragrostis plana
Eragrostis racemosa
Harpochloa falx
Heteropogon contortus
Hyparrhenia hirta
Panicum maximum
Paspalum notatum
Paspalum scrobitulatum
Setaria sphacelata
Sporobolus africanus
Sporobolus pyramidalis
Stiburus alopecuroides
Themeda triandra
Tristachya leucothrix
Urochloa panicoides