



Thèse présentée en vue de l'obtention du grade de docteur en sciences
agronomiques et ingénierie biologique

50 years of woody vegetation dynamics in the Senegalese Sahel (Ferlo): bases for a functional diversity approach

Morgane DENDONCKER

- defended on October 8, 2020 -

PhD dissertation committee:

Supervisor:	Caroline VINCKE	-	UCLouvain
Reviewers:	Charles DE CANNIERE	-	ULB
	Pierre DEFOURNY	-	UCLouvain
	Alexandre ICKOWICZ	-	CIRAD
	Christian MESSIER	-	UQAM
President:	Marnik VANCLOOSTER	-	UCLouvain

À Nicolas Najdowski

(1989-2017)

Merci pour tout ce que tu m'as offert

Acknowledgments

Remerciements

Mes premiers remerciements vont à ma promotrice, Caroline Vincke. *Caroline*, je n'aurais jamais réussi cette thèse sans toi. Merci du fond du cœur pour tout ce que tu m'as apporté, tant au niveau professionnel que personnel. Tu as partagé mes joies et tu m'as soutenue dans les moments les plus difficiles. Ta porte était toujours ouverte pour accueillir mes doutes et mes questionnements. Merci infiniment pour ton écoute, ta disponibilité, ta confiance, pour tes encouragements constants et ta capacité à me pousser dans mes réflexions tout en me freinant lorsque je voulais aller trop loin. Je n'aurais pas pu souhaiter de meilleure promotrice que toi ! Je garde de merveilleux souvenirs de nos deux séjours au Sénégal. Cette fin de thèse marque la fin d'une aventure mais également le début d'une nouvelle, et j'en suis tellement heureuse !

Je remercie *Charles De Cannière*, *Pierre Defourny*, *Alexandre Ickowicz* et *Christian Messier* d'avoir accepté de faire partie de mon jury de thèse, et dont les précieux conseils m'ont aidé à améliorer mon manuscrit. Merci à *Marnik Vanclooster* pour avoir accepté la présidence du jury. Je remercie également les membres de mon comité d'accompagnement : *Jan Bogaert*, *Christian Corniaux*, *Alexandre Ickowicz*, et *Sabine Miehe*.

Cette thèse est le fruit d'une collaboration étroite avec le *Pôle Pastoralisme et Zones Sèches* (PPZS, Dakar), qui m'a donné les moyens financiers et logistiques de réaliser mes missions sur le terrain ainsi que l'occasion de rencontrer de nombreux scientifiques. Merci à toute l'équipe de coordination du PPZS (dont *Astou Diao Camara* et *Paulo Salgado*). J'adresse également mes remerciements à l'*ISRA-LNERV* et à *Momar Talla Seck* pour l'accueil dans leurs locaux à Hann, ainsi qu'à la direction régionale du *CIRAD* de Dakar (*Denis Depommier* et *Sylvie Lewicki*).

Christian, merci pour les chouettes discussions, pour les traditionnels « café-chocolat-biscuits belges » partagés à chacune de mes arrivées au Sénégal et pour les soupers (merci également à *Maïté* pour son accueil chaleureux). Merci *Fatima*

pour ton aide dans l'administratif et la préparation de mes missions (sans oublier les beignets !), toujours avec le sourire et dans la bonne humeur. Merci à tous les chercheurs, doctorants, mémorants que j'ai eu l'occasion de côtoyer au PPZS : *Philippe Lecomte, Habibou, Bérénice, Myriam, Serena, Océane*. L'ambiance n'aurait pas été aussi bonne sans vous. *Serena*, merci à toi et à *Mamadou* de m'avoir accueillie chez vous et de m'avoir fait découvrir de nombreuses facettes de la vie quotidienne à Dakar.

Je remercie chaleureusement *Tamsir Mbaye* (ISRA) et *Daouda Ngom* (UCAD), pour m'avoir fait bénéficier de leur expertise et de leurs connaissances du terrain sahélien, leurs conseils précieux m'ont été des plus utiles dans ma recherche. Merci également à *Sékouna Diatta, Aziz Dionf, Ibra Touré, Marième Diallo, Amy Bakhoum* pour leur aide et à *Ousmane Ndiaye* pour son accueil à Dahra.

Cette thèse a nécessité de nombreuses missions sur le terrain durant lesquelles j'ai toujours été bien entourée. Un grand merci à *Moustafa Dia*, chauffeur et interprète, il est l'élément indispensable pour une mission réussie ! Merci à ceux qui m'ont accompagnée lors de mes inventaires, particulièrement *Amadou Sow*, éleveur, expert dans l'art du thé et botaniste, ses connaissances du terrain ont grandement facilité mes missions.

Simon, un immense merci ! Tu m'as accueillie comme une princesse chaque fois que je suis venue chez toi à Dakar. Merci pour les visites touristiques durant lesquelles tu m'as fait découvrir mille et un endroits « coups de cœur ». Au niveau professionnel, merci mille fois pour ton aide dans les analyses de végétation, pour nos discussions sur la diversité fonctionnelle, tes explications didactiques (vive les schémas et les cartes!) et pour avoir fait le « vrai » docteur-PhD dans les demandes de contact et de données.

Many thanks to the « Copenhagen team »: *Martin Brandt, Rasmus Fensholt and Kjeld Rasmussen* for their help in remote sensing analyses and their contribution to a paper. I look forward to continue our collaboration in the frame of the CASSECS project. I'd also like to thank *Jim Tucker*, from NASA, for providing the Worldview-1 images and for his contribution to one of my papers.

Merci à *Pierre Hiernaux* pour les discussions passionnantes à Copenhague et à Dakar, pour ton aide dans le choix de mes sites d'étude et pour ta relecture attentive d'un papier. Merci à *Mathieu Jonard*, pour son aide dans les analyses statistiques et à *Julien Radoux* et *Marie-Julie Lambert* pour leur aide en télédétection. Je tiens également à exprimer ma reconnaissance à différentes personnes qui m'ont aidée pour des travaux qui n'ont malheureusement pas pu être intégrés à

cette thèse, mais dont la continuation sera poursuivie : merci à *Olivier Bouchez*, *Hans Beeckman*, *Claire Delvaux*, *Kevin Lievens*, *Tom de Mil* et *Benoit Jourez* pour leur aide dans les analyses dendrochronologiques.

A tous mes collègues du labo *EFOR*, anciens et actuels, un tout grand merci pour la bonne ambiance quotidienne ! Particulièrement à *Camille G.*, merci mille fois pour ton enthousiasme, ton écoute et ton aide en toute circonstance, tu es une collègue en or ! A *Julie et Camille D.*, de m'avoir accompagnée dans mes petits délires. A la team C153 (*Hugues et Kristoffel*). A *Karine*, qui nous rappelle toujours que les pauses, c'est bien, les pauses avec tarte, c'est mieux ! Et à *Françoise*, toujours au petit soin pour l'équipe. Merci à toute la team *ACELI*, pouvoir partager son expérience avec d'autres doctorant·e·s est tellement précieux. Rien de tel qu'un petit *Unlock!* 3 jours avant la remise pour garder la forme ! Je remercie également les mémorant·e·s que j'ai eu l'occasion d'encadrer : *Delphine Fécherolle* et *Félix Laurent*.

Merci à toute ma famille, et particulièrement à mes parents, pour leur soutien et leur amour. *Maman*, la scientifique c'est toi ! Tu es la première à t'interroger sur la nature et tu m'as transmis cette passion. *Papa*, tu m'as transmis ta volonté de toujours aller au bout des choses et de ne jamais abandonner.

Nico, tu m'encourages depuis que je suis toute petite à chercher à comprendre le monde qui m'entoure et à en apprendre toujours plus. Tu as toujours été mon modèle, merci d'avoir été, et d'être toujours, un grand frère si attentionné. Je te remercie également pour toute l'aide que tu m'as apportée dans mes travaux de recherche et pour ton écoute à certains moments où je doutais de mon projet. *Jo*, ma grande sœur chérie, merci pour la façon dont tu as toujours veillé sur moi et encouragée, c'est un peu comme si j'avais un guide rassurant sur le chemin de la vie.

Sophie, quelle chance de t'avoir pour belle-sœur ! Merci pour toutes tes petites attentions, cartes, messages ou photos, ta gentillesse et ton accueil me font toujours chaud au cœur. *Mathieu*, merci pour les chouettes discussions « bois » et pour ton aide dans les petits traitements de mes rondelles. *Raphaël*, *Martin*, *Noah*, vous êtes mes petits rayons de soleil !

J'ai également été bien soutenue par mes amis. Merci à tout le groupe « les agros-bisounours » : *Albé*, *Rox*, *Camille*, *Cath* (lis aussi plus bas !), *Manon*, *Isa*, *Sara*, *David*, *Romain*, *Anne-So*, *Florine* et.... *Seb*, bien sûr, pour ta bonne humeur communicative qui a toujours été mon remède anti-déprime ! *Justine*, *Judith*, *Sophie*, les filles, merci pour les super moments d'évasion, les magnifiques

souvenirs (next summer : Avignon !) et pour vos encouragements, j'ai toujours pu compter sur vous ! Merci à tout le *groupe de théâtre* et de l'école du spectateur, rien de tel qu'un petit verre à Liège pour se remettre d'une semaine difficile. Un merci spécial à *Nico* (*alias* Michel, Hyppolite et bien d'autres encore !) pour tous ces fous rires en répétition ! Merci aussi à *Laurie*, tu ne t'en es peut-être pas rendue compte mais tu m'as énormément aidée dans une phase critique !

Je termine enfin par mes deux merveilleuses amies qui ont supporté mes sautes d'humeur durant de long mois de finalisation. *Cath*, tu comptes parmi mes meilleures supportrices, capitaine de la Momo team ! Merci pour tous tes encouragements et les partages de petits faits divers et blagues (vive les « chotor morph » ou chameaux-poulets !) qui égayaient mes longues journées ! Et enfin, *Olive*, merci du fond du cœur, pour tout, je ne sais pas ce que j'aurais fait sans les nombreux coups de téléphone, séances de coaching et « hug » réconfortants (« c'est ma bulle ! ») qui m'ont vraiment permis de tenir le coup lors de la dernière ligne droite.

Cette thèse a été financée par une bourse FSR suivie d'une bourse FRIA (F.R.S.-FNRS, Belgique).

DigitalGlobe very high-resolution commercial satellite images were acquired through NASA under the NextView Imagery End User License Agreement. The copyright remains with DigitalGlobe and redistribution is not possible

Summary

Sahelian woody vegetation has been the topic of many researches since the great drought that struck the Sahel in the 1970s-1980s. However, there is currently no consensus about the long-term trends of these savannas, as observations sometimes seem contradictory, according to the indicators used. Moreover, the observed trends often lack an understanding of the consequences on ecosystem functioning and subsequently on the provision of ecosystem services (ES), even if a decrease in ES is often assumed. As the Senegalese sylvo-pastoral zone of the Ferlo is the home of pastoralists that rely on these ES in their daily life, it is crucial to be able to predict the woody vegetation response to the current pressures acting on these ecosystems. Even more as some of these pressures (climatic and anthropogenic) are forecasted to increase in the near future.

In this research, we investigate the long-term trends of woody vegetation in the sylvo-pastoral zone of Senegal in order to discuss its persistence and its effects on two ecosystem functions (primary productivity and biogeochemical cycles) when facing three types of disturbances (drought, fire and grazing). Our study area is located in the Ferlo, around two deep-wells, Widou Thiengoly and Tessékéré. The area suffered from intense and recurrent droughts from the 1970s to the 1980s, this period being commonly called the “great drought”, with extreme consequences on livestock mortality, crop yields and on the woody vegetation.

This vegetation is examined during three periods (from 1965 to 1971; 1972-1984; 2015-2018) using different indicators of the vegetation state, its trajectory and its persistence, computed at several spatial scales. We relied on multiple datasets and we mobilized several disciplinary angles to gather complementary information and achieved three specific objectives. First, we studied the spatial differentiation of the current woody vegetation according to the topography, used as proxy for water availability. Second, we evaluated woody vegetation changes since 1965 onward in terms of specific composition, density and woody cover. Third, we transposed the different indicators from the first two specific objectives into a functional level of the woody communities.

Field inventories were carried out to characterize the current state of woody vegetation regarding the specific composition, the density and the population structure. The historical vegetation database Flotrop, provided information about species composition from 1970 to 1986. Earth observation datasets were used to assess the temporal changes in density and woody cover since 1965. Finally, traits data collected in the literature allowed to study the (past and current) vegetation response to drought, grazing and fire, and the vegetation effects on the primary productivity and the biogeochemical cycles.

The combination of old high-resolution satellite imagery and aerial photos outlined a decrease in woody plant density from 14.8 trees.ha⁻¹ in 1965 to 11.9 trees.ha⁻¹ in 2008, but showed a stabilization this last decade, reaching 12.2 trees.ha⁻¹ in 2018. Taking into account the bushes and shrubs (through field inventory carried out in 2015), the overall density reached 42.5 ind.ha⁻¹. However, we observed a change in species composition from ancient records to recent inventories, with an increase of the proportion of shrub species compared to trees. Changes in species frequency revealed that 13 species (out of 40) were decreasing, while six remained stable, the others being too scarce to conclude about their trends.

We inventoried 24 species within our study area. Yet, current woody communities are dominated by a few species, like *Balanites aegyptiaca*, *Boscia senegalensis* and *Calotropis procera*, which together occupy 82.5% of the woody stand in terms of density. While these dominant species are omnipresent, local topography strongly influences species composition and density parameters. On tops, the three dominant species are accompanied by *Sclerocarya birrea* and *Acacia tortilis*, while in depressions, the secondary species are *Grewia bicolor*, *Acacia seyal* and *Sclerocarya birrea*. Overall, taxonomic and functional richness, density (of adults and regeneration) and woody cover are higher in depressions. Yet, the future of many populations of secondary and rare species is unsecured, as we observed a lack of regeneration for most of them.

Species with stable abundances from 1970 to 2015 present a different drought response strategy than the declining species. The great drought has selected species, favoring the traits combination of a long leafing period (more evergreen or semi-evergreen species), small vessel area and heavy seeds. Current communities also tend to contain smaller trees. In addition, we observed a decline of functional redundancy and response diversity for the functional effects groups of primary productivity and biogeochemical cycles.

As response diversity is currently extremely low for some functional effect groups, the persistence of these groups is uncertain. Even more with the low regeneration exhibited by some currently abundant species that are the only representatives of these groups. As the two studied functions support several ecosystem services, we propose some target species to protect in order to maintain the effects of these species on the ecosystem. Finally, given the major role of topography on current vegetation and that depressions harbor communities with a higher response diversity, we suggest that future research focus on these diversity hotspots. Indeed, a better characterization of their soil hydric properties, their functional diversity and their connectivity at the landscape scale could help supporting the persistence of woody vegetation.

Acronyms and abbreviations

AI	Aridity index
APG	Angiosperm Phylogeny Group
AVHRR	Advanced Very High Resolution Radiometer
CSE	Centre de Suivi Ecologique
CWM	Community weighted mean of trait values
ECE	Extreme climatic event
EO	Earth observation
ES	Ecosystem services
FD	Functional diversity
FD _{is}	Functional dispersion index
FD _{iv}	Functional divergence index
FE _{ve}	Functional evenness index
FG	Functional group
FR _{ic}	Functional richness index
GHCN	Global Historical Climatology Network
GPS	Global Positioning System
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IPCC	Intergovernmental Panel on Climate Change
IRD	Institut de Recherche pour le Développement
IVI	Importance Value Index

JISAO	Joint Institute for the Study of the Atmosphere and Ocean
MEA	Millenium Ecosystem Assessment
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalized difference vegetation index
NOAA	National Oceanic and Atmospheric Administration
PCA	Principal components analysis
PCoA	Principal coordinates analysis
PPZS	Pôle Pastoralisme et Zones Sèches
RUE	Rain use efficiency
SCD	Size class distribution
SDII	Simple Daily Intensity Index
SLA	Specific leaf area
SPI	Standardized Precipitation Index
TEEB	The Economics of Ecosystems and Biodiversity

Table of contents

Chapter 1 Introduction	19
1.1. General introduction	20
1.2. Objectives and outline.....	25
Chapter 2 State of the art	31
2.1. Sahelian ecosystems	32
2.1.1. The bioclimatic zones in West Africa	32
2.1.2. Sahelian climate	32
2.1.3. Determinants of Sahelian vegetation	35
2.2. The Ferlo: sylvo-pastoral zone of Senegal	37
2.2.1. Study area.....	37
2.2.2. Pastoralism: variable resources and mobility	39
2.2.3. Ecosystem services provided by woody vegetation.....	41
2.2.4. A brief overview of frequent woody species in the Ferlo	42
2.3. Persistence and resilience: what are we talking about?.....	49
2.3.1. Concepts and definitions	49
2.3.2. Resilience and persistence in this research.....	51
2.4. Functional diversity.....	51
2.4.1. A functional approach of communities	51
2.4.2. Functional diversity components and related indices.....	55
Chapter 3 Materials and methods.....	59
3.1. General methodology: a multidisciplinary approach within the field of ecology	60
3.2. Bio-physical, climatic and human context of the study area	61
3.2.1. Geomorphology, soils and vegetation	61
3.2.2. Soils hydric properties	63
3.2.3. Climate data.....	67
3.2.4. Populations and livestock	73
3.3. Description of the datasets	75
3.3.1. Field inventory dataset.....	75
3.3.2. Flotrop: an historical vegetation database	77
3.3.3. Geographical and remote sensing dataset	78
3.3.4. Species functional traits dataset	80
3.4. Summary: datasets, methods and chapters.....	84

Chapter 4 Spatial variability of current woody vegetation and its regeneration.....	85
4.1. Introduction.....	87
4.2. Material and methods.....	89
4.2.1. Study area.....	89
4.2.2. Sampling and inventory measurements	91
4.2.3. Data analyses.....	94
4.3. Results.....	98
4.3.1. Influences of environmental factors on structure, composition and regeneration	98
4.3.2. Regeneration features	103
4.4. Discussion	108
4.4.1. Influence of environmental factors	108
4.4.2. Population structure and regenerative capacity.....	110
4.4.3. Persistence of woody plant population.....	114
4.5. Conclusion	115
4.6. Complementary analyses.....	116
4.6.1. Methodology	116
4.6.2. Results and discussion	117
4.6.3. Partial conclusion	118
Chapter 5 Woody vegetation changes from 1965 to 2018.....	123
5.1. Introduction.....	125
5.2. Material and methods.....	127
5.2.1. Study area, indicators and datasets	127
5.2.2. Woody cover and density changes	129
5.2.3. Dynamics in species composition.....	132
5.3. Results.....	135
5.3.1. Woody plant density	135
5.3.2. Woody cover.....	135
5.3.3. Species composition dynamics.....	138
5.4. Discussion	140
5.5. Conclusion	143
Chapter 6 A trait-based approach of woody vegetation	145
6.1. Introduction: functional diversity and ecosystem functioning	146
6.2. Methodology.....	149
6.2.1. The response-effect trait-based approach: overview.....	149
6.2.2. Response and effect traits	150
6.2.3. Assessing functional diversity: computing FD indices.....	154
6.2.4. Traits and functional diversity analyses: overview	156
6.2.5. Temporal changes in species traits and FD	158
6.2.6. Influence of topography on current functional diversity.....	163
6.3. Results.....	163
6.3.1. Trait matrix from literature review	163
6.3.2. Temporal changes	167

6.3.3. Influence of topography on current functional diversity.....	179
6.4. Discussion	184
6.4.1. Influence of topography on current functional diversity.....	184
6.4.2. Changes in species pool, traits combination and FD	186
6.4.3. Functional redundancy and response diversity.....	189
6.4.4. Strengths and limitations of the approach	191
6.5. Conclusion	195
Chapter 7 General discussion and conclusion.....	199
7.1. Key findings	200
7.2. Persistence indicators	206
7.2.1. Ecological situation.....	206
7.2.2. Persistence, ecological resilience and constancy.....	207
7.2.3. Variables and indicators	208
7.2.4. Persistence of the studied functional effects.....	210
7.2.5. How to ensure persistence?	213
7.3. Vegetation long-term dynamics after an extreme climatic event	218
7.4. Perspective for future research	220
7.5. Conclusion	222
Appendices	223
Appendices to Chapter 2.....	225
Appendices to Chapter 3.....	239
Appendices to Chapter 4.....	267
Appendices to Chapter 5.....	271
Appendices to Chapter 6.....	287
Appendices to Chapter 7.....	297
Bibliography	299
Curriculum vitae	327

Chapter 1

Introduction

1.1. General introduction

Drylands biomes are usually identified based on the aridity index (AI) which is the ratio of average annual precipitation and mean annual potential evapotranspiration. The areas presenting an AI inferior to 0.65 are considered as dry and represent 41.5% of the global terrestrial area (Bastin *et al.*, 2017). Among drylands, four categories are distinguished, according to the AI values: the hyper-arid lands ($AI < 0.05$), the arid lands ($0.05 < AI < 0.2$), the semi-arid lands ($0.2 < AI < 0.5$) and finally the dry subhumid lands ($0.5 < AI < 0.65$) (FAO, 2019). A third of these drylands are located in Africa, covering nearly two billions of hectares (FAO, 2019). They are the home of about 41% of the African continent population (Reynolds *et al.*, 2007).

Among drylands, savannas are biomes characterized by the coexistence of a tree and a grass layer (Sankaran *et al.*, 2005). Tropical savannas cover between 12.5% and 20% of the global land surface and half of the African continent (Pennington *et al.*, 2018; Scholes and Archer, 1997). In these ecosystems, the maximum woody cover level is limited by the mean annual rainfall when this variable is below 650 mm. The interaction of fire, herbivory and soil properties often keeps the actual woody cover below this maximum threshold (Sankaran *et al.*, 2005).

The Sahel is an African bioclimatic region that belongs to drylands and where savanna is the typical vegetation formation. This bioclimatic region receives an amount of annual rainfall of (100-) 200 to 600 mm, which means that the maximum woody cover is limited by rainfall (Sankaran *et al.*, 2005). This amount of water falls during a short rainy season, from July to October. The Sahelian savannas comprise a grass layer largely dominated by annual species (perennial grasses are rare) and a perennial woody layer (Hiernaux and Le Houérou, 2006). Woody species usually encountered between 200 to 400 mm of annual rainfall are the spiny *Acacia* sp. and other spiny species such as *Balanites aegyptiaca* (L.) Del. and *Ziziphus mauritiana* Lam. (Le Houérou, 1980d). The availability of water, through the combination of topographic and edaphic variations, plays a key role in the differentiation of structure and composition of herbaceous and woody vegetation (Dembélé *et al.*, 2006; Hiernaux and Le Houérou, 2006).

The Millennium Ecosystem Assessment (MAE) identified five main drivers responsible for the changes in biodiversity and ecosystems over the past 50-100 years: habitat change, climate change, invasive species, over-exploitation and pollution (MEA, 2005). Climate change is already affecting many ecosystems across the five continents and was pointed out as a driver with a “rapid increase”

trend for tropical grasslands and arid savannas (MEA, 2005). Besides, savannas are identified as being part of the most sensitive ecosystems “to future changes in land use and climate” (Sankaran *et al.*, 2005).

One of the consequences of climate change is the increase in frequency of intense droughts. The Intergovernmental Panel on Climate Change (IPCC) emphasizes that water scarcity will particularly be exacerbated in semi-arid environments of Africa, leading to negative consequences on agricultural systems (with a high confidence level; Mirzabaev *et al.*, 2019). Yet, drought response of savannas has received less attention than the drought response of forests and temperate grasslands (Sankaran, 2019). One exception of intensively studied climatic event is the great drought that struck the Sahel during the 1970s-1980s. This episode is the most severe drought of the 20th century for this region regarding its length and its intensity. The reduction of the rainfall between 1970 and 1989 attained 20 to 40% compared to the long term mean (1901-1998; Nicholson, 2001) with some severe consequences on woody vegetation, livestock mortality and crop yields, leading to famines in several Sahelian countries (Epule *et al.*, 2014; Nicholson *et al.*, 1998). Elevated mortality rates of woody vegetation have been reported in several parts of the Sahel (e.g. Hiernaux *et al.*, 2009; Le Houérou, 1989; Poupon, 1980). This drought is an extreme climatic event (ECE) following Smith (2011) who suggests that this term should be used only if the “extremeness” is present both in the driver and in the response. She defined an ECE as “an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability”. In addition to this ECE, annual rainfall in the Sahel is following a decreasing trend since 1900 (Figure 2.2).

In addition to the climatic constraint, the population in drylands of Africa is expected to exceed one billion people by 2050, with an estimated population of 0.6 billion in 2016 (Mirzabaev *et al.*, 2019), in regions where the dependence of people livelihood to woodlands or grasslands is strong (FAO, 2019). Indeed, Sahelian vegetation (both trees and grasses) provides numerous ecosystem services (ES) to the population. Some of them are of particular direct importance. Fodder is arguably the most important one, as the pastoralism is the principal source of livelihood (Le Houérou, 1980d; Thébaud and Batterbury, 2001). Livestock eat grasses from the beginning of the rainy season until the middle of the dry season when it turns to foliage and bark of trees and shrubs until the next rainy season. Trees and shrubs also provide firewood, wood as material, food, and other regulation services. The importance of these ES is pointed out by the IPCC report on climate change and land, which identifies the pastoral and

agropastoral households in drylands as a key vulnerable group (Mirzabaev *et al.*, 2019). Moreover, livestock numbers have been increasing in the Sahel due to a combination of better access to water through modern infrastructure and improvement of veterinary care, and this despite the high mortality rates observed during the 1970s-1980s drought (Ickowicz *et al.*, 2012; Sinclair and Fryxell, 1985; Thébaud, 1990; Touré, 1990). The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) summarizes these pressures for the Sahelian grazing lands, stating that they “have suffered much damage in the past 50 years, through an increasing human population, excessive advance of cropping into very marginal areas and serious deforestation, mainly for firewood, all exacerbated by recurrent droughts” (IPBES, 2018). Sahelian woody vegetation is indeed also submitted to an increasing anthropic pressure.

After the great drought, high mortality rate of woody vegetation and a decrease in species richness have been reported throughout the Sahel (e.g. Gonzalez, 2001; Poupon and Bille, 1974; Wezel and Lykke, 2006). Changes in the herbaceous layer have also been observed, with for instance the disappearance of the perennial grasses that were previously occasionally present in the southern Sahel (Le Houérou, 1989). Since then, research has continued to draw the recent tendency of vegetation for the period after the drought, either by field studies (Hiernaux *et al.*, 2009; Mieke, 2002; Vincke *et al.*, 2010), remote sensing (Brandt *et al.*, 2017; Olsson *et al.*, 2005), local knowledge (Lykke *et al.*, 2004), or a combination of these methods (Brandt *et al.*, 2014; Herrmann and Tappan, 2013; Lykke *et al.*, 1999).

The multiplicity of field areas interested in the long-term trends of vegetation induces the existence of numerous indicators used to monitor this vegetation (e.g. tree density, woody cover, species richness, NDVI¹), which in turn can lead to debate about the trends. This is also one of the causes of the still ongoing debate about desertification² and degradation, a widely used term in the literature on drylands vegetation dynamics; particularly since the renewed attention after the great drought and its dramatic consequences on environment and livelihood.

¹ NDVI is a spectral index calculated after the red and infrared satellite bands, based on the reflectance of the photosynthetic tissues in the near infrared and red wavelengths.

² Desertification is defined by the United Nations as “land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors, including climatic variations and human activities” (UN, 1992) or as a “process of land degradation that reduces its productivity” (Nicholson *et al.*, 1998).

This partially explains why results sometimes seems contradictory. On the one hand, some researches show a degradation of Sahelian vegetation and on the other hand, some argue that no degradation is occurring, relying on greening observation (i.e. an increasing trend in the vegetation greenness). Among the studies that indicate a likely degradation, Hein and De Ridder (2006) claim that an anthropogenic degradation of Sahelian vegetation is likely. Gonzalez (2001) stated that the changes in species composition observed through field inventory combined with the decreasing in density are evidence of land degradation in the West African Sahel. The studies showing that no degradation is occurring in the Sahel (e.g. Prince *et al.*, 1998) or that a greening phenomenon is occurring since the 1980s (Anyamba and Tucker, 2005; Dardel *et al.*, 2014; Herrmann *et al.*, 2005; Olsson *et al.*, 2005), mostly used the NDVI time series, the NDVI detecting vegetation greenness and quantity. For instance, Anyamba and Tucker (2005) showed a greening for the period 1994-2003 compared to 1982-1993, indicating a recovery from the great drought. Many authors agreed that the increase of rainfall during the 1990s, though still far from the rainfall conditions from 1930-1965, is the principal cause of this greenness, though other factors can be involved such as soil types and human influence (Brandt *et al.*, 2015)³. Regarding the meaning of this greening at ground level, Herrmann and Tappan (2013) pointed out a decrease in species composition along the disappearance of large trees. Even if Anchang *et al.* (2019) showed that it was mainly the woody component that was responsible for the greening phenomenon, the characterization of the relative part of herbaceous and woody vegetation in this greening needs more investigations. But the lack of *in situ* vegetation data is outlined by Mougin *et al.* (2009) and Mbow *et al.* (2015) and few studies relying only on field data are dealing with long-term dynamics (Hiernaux *et al.*, 2009; Vincke *et al.*, 2010).

In addition to the issue of which indicator is used to monitor vegetation changes, the conclusion of these studies also vary according to the spatial (local vs regional) and temporal scales. Rasmussen *et al.* (2016) highlight that, despite many researches during these last decades, no consensus exists about environmental changes in the Sahel. They stated that there is still debate and contradictions around three topics: degradation and desertification; changes in land use and land cover; climate change and climate variability. They further give a list of five possible causes for these apparent contradictions: the inconsistency of the concepts such as degradation and land cover (e.g. the imprecise definitions, also

³ For more references on these contrasting evidence on vegetation dynamics, see Hänke *et al.* (2016).

outlined by Herrmann and Hutchinson, 2005); the discipline bias in the choice of indicators or study sites; the strategic bias (e.g. in the case of field survey, respondents may hope to attract development aid); the methodological bias (spatial and temporal scale, datasets used, studied variables); and the sampling bias.

Furthermore, the context in which the desertification debate is occurring has evolved since its first use (attributed to Aubréville, 1949) along with our understanding of some of the processes involved (Herrmann and Hutchinson, 2005). For instance, rangeland ecology has been explained by two types of paradigms: equilibrium vs non-equilibrium (see Briske *et al.*, 2003 for detailed comparison). The equilibrium theory states that each rangeland has a unique persistent state (climax) and that grazing lead the system to an opposite direction of the successional trend (Herrmann and Hutchinson, 2005). The consequence is that there is an equilibrium for a given stocking rate. Low rainfall impacts the system in the same way than grazing (i.e. opposite to the succession) and high rainfall accelerates succession (Westoby *et al.*, 1989). The non-equilibrium theory argues that the vegetation composition is driven by the occurrence of stochastic events that could result in changes that are not always reversible (Herrmann and Hutchinson, 2005; Milton *et al.*, 1994).

Briske *et al.* (2003) stated that both paradigms are not mutually exclusive and that equilibrium and non-equilibrium dynamics can occur in systems, depending on the spatio-temporal scales considered for the dynamics evaluation. For instance, Miede *et al.* (2010) showed that conditions of both equilibrium and non-equilibrium applied on herbaceous layer productivity and composition during a 27 years period in Senegalese rangelands.

Altogether, when talking about vegetation long-term trends, it is therefore crucial to precise the observation period, the spatial scale (trends detected at the regional scale might not be detected at the local scale), and the indicators used.

Given these multiple constraints and the critical importance of ES provided by woody vegetation, the current challenge in the Sahel, is to assess if these ecosystems will persist in such state that they are able to regenerate on the long-term and still provide ES that underpin the sylvo-pastoralism as land use.

1.2. Objectives and outline

The main objective of this work is to evaluate the woody vegetation dynamics from 1965 to 2018 in the Ferlo, the Sahelian sylvo-pastoral zone of Senegal, in order to discuss the persistence of this vegetation, and of its effects on two ecosystem functions (primary productivity and biogeochemical cycles) when facing three types of disturbances (drought, fire and grazing).

To achieve the main objective, we address three questions. First, what is the state of current woody vegetation? This state is assessed through different indicators: species composition, density, woody cover, population structure and regeneration. Second, what are the changes that have occurred since 1965 on the density, woody cover and species composition? Third, how can these indicators be transposed to the level of ecosystem processes (i.e. what are their effects on ecosystem functioning) and how do they influence the response of woody vegetation to pressures? A trait-based approach is therefore applied to analyze the effects of woody communities on ecosystem processes (primary productivity and biogeochemical cycles), along with the response of this vegetation to the pressures of drought, grazing and bush fire. This kind of approach has the potential to assess the interactions between a large number of species and their environment (Garnier and Navas, 2012). Moreover, it is currently rare for arid and semi-arid zones, especially for the Sahel, for which, to our knowledge, no research has yet focused on functional diversity of woody vegetation.

As stated earlier, the study of vegetation dynamics and its persistence requires a clear characterization of the ecological situation through several checkpoints suggested by Grimm and Wissel (1997). The first element to clarify is what is being studied, i.e. the ecological level and the variables of interest. In this study, our focus is on the woody vegetation, studied at the community level (i.e. local assemblage of species, an inventory plot for instance) and at the regional scale (the study area). The variables of interest are the woody vegetation indicators listed in the above paragraph.

The second point is to define the spatial and temporal scales at which the assessment is carried out. The spatial reference is our study area (65 km x 58 km; as defined in section 2.2.1) located around two deep wells, Widou Thiengoly and Tessékéré (Figure 1.1). These permanent water points belong to a network of hydraulic structures dug in the 1950s and covering all Ferlo. Since the implantation of modern hydraulic infrastructures, the pastoralists and their herds have had access to pastures throughout the year (Touré, 1990). This has led to

changes in the patterns of annual transhumance, with sometimes the permanent installation of pastoralists in small settlements in the vicinity area of deep wells, increasing pressure on the vegetation. The maximal spatial extent of the validity domain is the “sylvo-pastoral reserve of the six deep wells” (Figure 1.1). The period of interest extends from 1965 to 2015-2018. As the great drought (1970s-1980s) is considered as an extreme climatic event, our temporal analyses are presented following a partitioning of the study period in three: before the great drought (1965-1971), during the drought (1972-1984) and after the drought (2015-2018). Despite this division, we do not assume that the great drought is the key driver to all the observed changes in the woody vegetation.

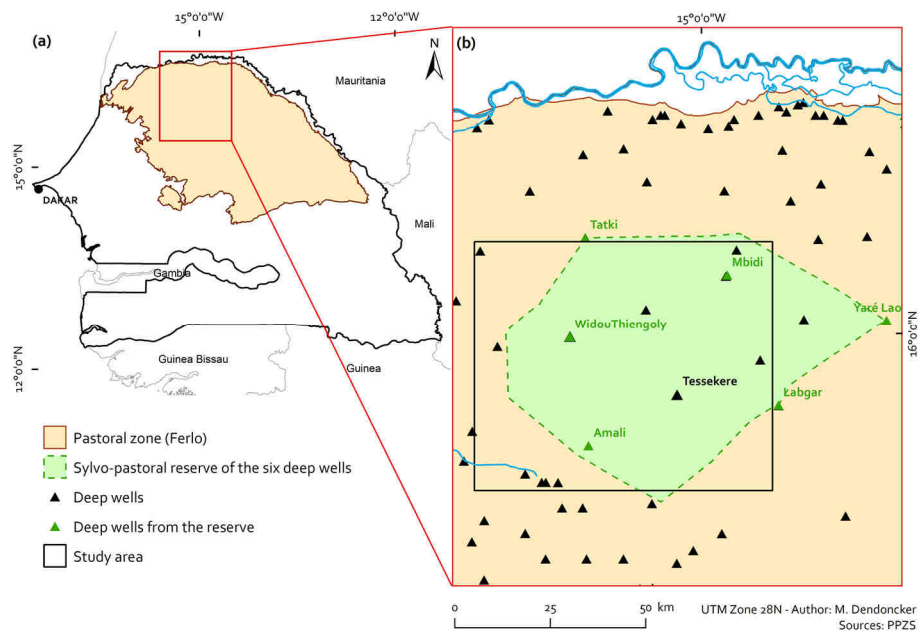


Figure 1.1 – (a) Location of the sylvo-pastoral zone (Ferlo) within Senegal; (b) zoom on the study area and the “sylvo-pastoral reserve of the six deep wells”.

The third point is the description of the reference state, that is, what we consider as the “normal” state of the system. In a system that may present conditions of both equilibrium and non-equilibrium, we choose to define this “normal” state as the one that allows the persistence of the extensive sylvo-pastoralism land use by maintaining the ES that support this land use (e.g. fodder provision, maintenance of soil fertility).

Finally, the fourth point is the listing of the environmental pressures that are applying on the studied variable (i.e. the woody vegetation). We distinguish the anthropogenic pressure, which includes the influence of human on woody vegetation either due to grazing or direct uptake, the climatic pressure (frequency of drought, increasing temperatures) and other “external” pressure such as bush fires.

The three above-mentioned research questions underlying our main objective are called “specific objectives” from now on (Figure 1.2). The first specific objective is the study of the spatial differentiation of the current vegetation according to the topography, used as proxy for water availability. Indeed, the soil composition and subsequently its hydric properties change along the topography, and run-off will modify the water balance following the toposequences. An extensive fieldwork was carried out around the two deep wells (139 plots of 0.25 ha), taking account of their proximity to the inventory plots to include a potential grazing gradient. The effect of topography is evaluated through different indicators: density, woody cover, species composition, regeneration rate, and population structure. Two hypotheses are being tested: (i) low topographic positions enhance woody vegetation density, regeneration and species richness; (ii) the proximity of deep wells, through higher wood collection and grazing, lower the density, regeneration and species richness.

The second specific objective is the evaluation of woody vegetation changes since 1965 onward in terms of specific composition, density and woody cover. This objective relies on two types of datasets: field data and Earth observation, (EO) data. The year 1965 is chosen as a starting point, as it is the date of the most ancient data source in our possession. Our observations are carried out at two different spatial scales within the study area. First, specific study sites have been located on dunes (6 sites of 1 km²), plains (6 sites of 1 km²) and near settlements (5 sites of 1 km²), for density and woody cover changes. Second, the changes in species composition are assessed at the study area scale using historical botanical surveys. The reason for this change of scale is the location accuracy of the historical surveys that would not allow their positioning on the field at less than 1.8 km. We tested the hypothesis that the location of the sites (dunes, plains, near camps) and hence the macrorelief and human activity has influenced the evolution of woody vegetation.

The third specific objective is to transpose the different indicators obtained from the first two specific objectives into a functional level of the woody communities, in order to address: (i) the woody vegetation capacity to respond to three

pressures: droughts, seen as extreme climatic events (i.e. not the annual succession of seasons), grazing by livestock (cattle, sheep, goats) and bush fires; (ii) the effects of this vegetation on two ecosystem functions: primary productivity and biogeochemical cycles. Response and effect of woody vegetation are analyzed through its current pool of functional traits and how this pool of traits has evolved since the period previous to the great drought, at the scale of study area (regional scale) and at the scale of communities (local assemblages of species). We hypothesize that (i) species (response and effect) traits combinations and functional diversity of communities have changed within the study area since 1965; (ii) and that functional diversity (of both response and effects traits) of the woody communities is different according to the topography.

The long-term trends of woody vegetation are studied through multiple disciplinary angles, using various methodologies and datasets. The core of this work relies on ecology but forestry and geomatics are also mobilized. Three types of datasets are at the basis of our analyses: field data (field inventory carried out in the frame of this research and historical botanical surveys from a vegetation database), EO data (aerial photos and satellite images), and literature data on species functional traits.

The integration of multiple datasets enables us to have a more complete view of the trajectory of woody vegetation compared to what we could have had focusing on one type of data only. Indeed, indicators derived from these datasets offer insight at different spatial and biological scales (community vs regional) and cover a longer time span. The other originality of this work is that it builds on numerous literature data, sometimes not published, about species traits and botanical surveys.

The document is organized in seven chapters, including the present introduction (Figure 1.2). Chapter 2 presents the bioclimatic context of Sahelian ecosystems and the state of the art about long-term vegetation trends. It also introduces the concepts underlying the main objective, i.e. resilience/persistence and functional diversity. Chapter 3 explains the general approach adopted for this work and the articulation of the different methodologies and datasets used in this thesis: field data, Earth observation data and literature data. Methodological details about sampling and analyses are embedded inside the corresponding chapters. Chapters 4 to 6 each refer to one of the three specific goals. Chapter 4 and 5 are based on submitted papers to which we have added some additional results. Chapter 7 first summarizes the main findings. Then, we discuss the different indicators measured in Chapters 4 to 6 in order to assess the persistence of both woody

vegetation and its effects on the two studied ecosystem functions. Based on this discussion, we suggest avenues for a potential management. We finally establish perspectives for future research.

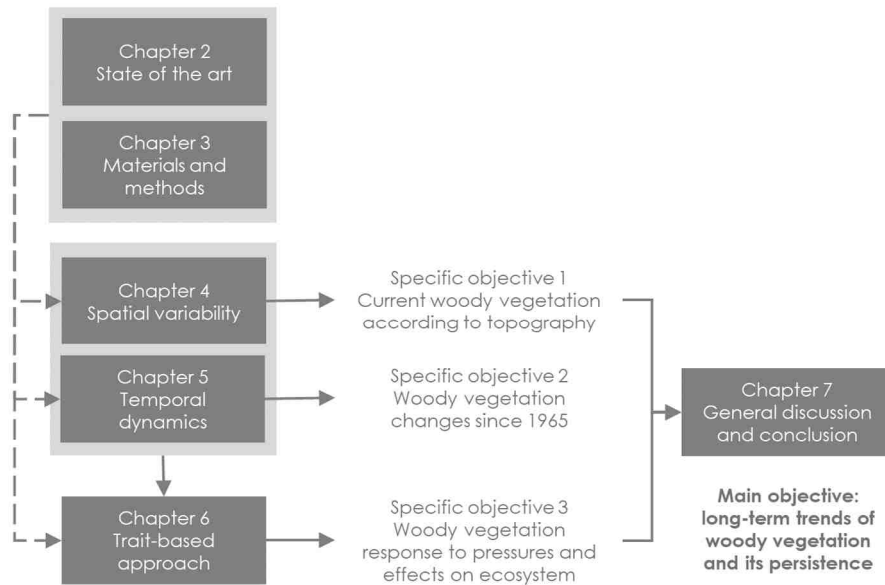


Figure 1.2 – Objectives and PhD outline. Chapters 2 and 3 establish the bases for Chapters 4 to 6, which each deal with one specific objective. Chapter 4 and 5 also underlie Chapter 6.

Finally, we wish to establish some terminology conventions for the sake of clarity. First, the term «vegetation» used in this document refers to the woody component unless stated otherwise. Second, species name are fully written (genus, species, botanical authors) the first time they appear in the text. Thereafter, they are named by either the combination of genus and species or only the genus if the species is the only representative. Third, references for databases are given only the first time the database is mentioned in a Chapter. Fourth, the terms “system” and “ecosystem” refer to the concept of socio-ecological system, as defined by Gallopin (2006): “the system that includes societal (human) and ecological (biophysical) subsystems in mutual interaction”. Finally, the mention of “great drought” points to the severe drought that struck the Sahel from the 1970s to the 1980s.

Chapter 2

State of the art

– *Outline* –

In this chapter, we describe the main elements of the geographical and biophysical context and introduce some key ecological concepts that are necessary to set the analytical framework of this research. First, Sahelian ecosystems are presented through a climate and vegetation description. Then, the particular context of the Sahelian sylvo-pastoral zone of Senegal, the Ferlo, is detailed. As debate about the temporal dynamics of the Sahelian vegetation is still ongoing, we summarize the two major trends that are discussed in the literature: the degradation of Sahelian vegetation vs the “greening” phenomenon. Finally, three concepts that underlie this thesis are presented: resilience and persistence, and functional diversity.

2.1. Sahelian ecosystems

2.1.1. The bioclimatic zones in West Africa

The bioclimatic zone of the Sahel covers the lands that lie immediately south of the Sahara desert. It stretches across whole Africa over a distance of 5000 km, from Senegal to the Red Sea (Figure 2.1). Its boundaries correspond to the mean isohyets of 100 mm or 200 mm northward (depending on the author) and the 500 to 700 mm isohyets southward (Nicholson, 1995). The precipitation regime presents a distinct dry season that lasts 8 to 9 months. As rainfall is expected to vary over time, isohyets and subsequently Sahel limits don't have a fixed position (Nicholson, 1995).

South to the Sahel, two other bioclimatic regions in West Africa are encountered. Their boundaries, like the Sahel, are not rigid but form a continuum along a climate and vegetation gradient. Between 600 and 1200 mm.year⁻¹, we enter the Sudanian bioclimatic region (Figure 2.1) where the dry season lasts 5 to 7 months. Vegetation is denser and the annual Sahelian grasses are replaced by perennial grasses, it is the domain of wooded savannas and open woodlands (CILSS, 2016). The Guinean region lies further south (Figure 2.1), between 1200 and 2200 mm.year⁻¹ but still with a distinct dry season of 7 to 8 months. The trees are taller (18-20 m) and the vegetation formation is a closed canopy forest (CILSS, 2016). In Senegal, the three bioclimatic zones cross the country from north to south. The more we move south, the denser the tree layer becomes, up to the formation of a closed canopy forest in the southern part (Figure 2.1).

The Sahelian zone can be further divided in 3 eco-climatic subzones (Hiernaux and Le Houérou, 2006; Le Houérou, 1989). From north to south, we pass through the Saharo-Sahelian transition zone (also called north Sahelian) between 100 and 200 mm of annual rainfall; the Sahelian zone *sensu stricto* between 200 and 400 mm and finally the Sudano-Sahelian transition zone between 400 and 600 mm (or south Sahelian).

2.1.2. Sahelian climate

The Sahelian climate is tropical arid to semi-arid with a monomodal rainfall pattern (Le Houérou, 1989). Rainfall depends on the West African monsoon, the circulation regime that emerges from the contact between the hot and wet intertropical air mass and the hot and dry Saharan subtropical air mass (Hiernaux

and Le Hou  rou, 2006; Nicholson, 2013). During June, the monsoon is moving northward during the boreal summer, thus bringing rain in West Africa, and southward during the austral summer (Nicholson, 2013). The wet season lasts four months, from July to October, with a rainfall peak in August (Nicholson, 2005). The temporal and spatial variability of rainfall is high with a coefficient of variation ranging between 32-43% for a rainfall regime of 200 to 400 mm.year⁻¹ (Hiernaux and Le Hou  rou, 2006; Nicholson, 1995).

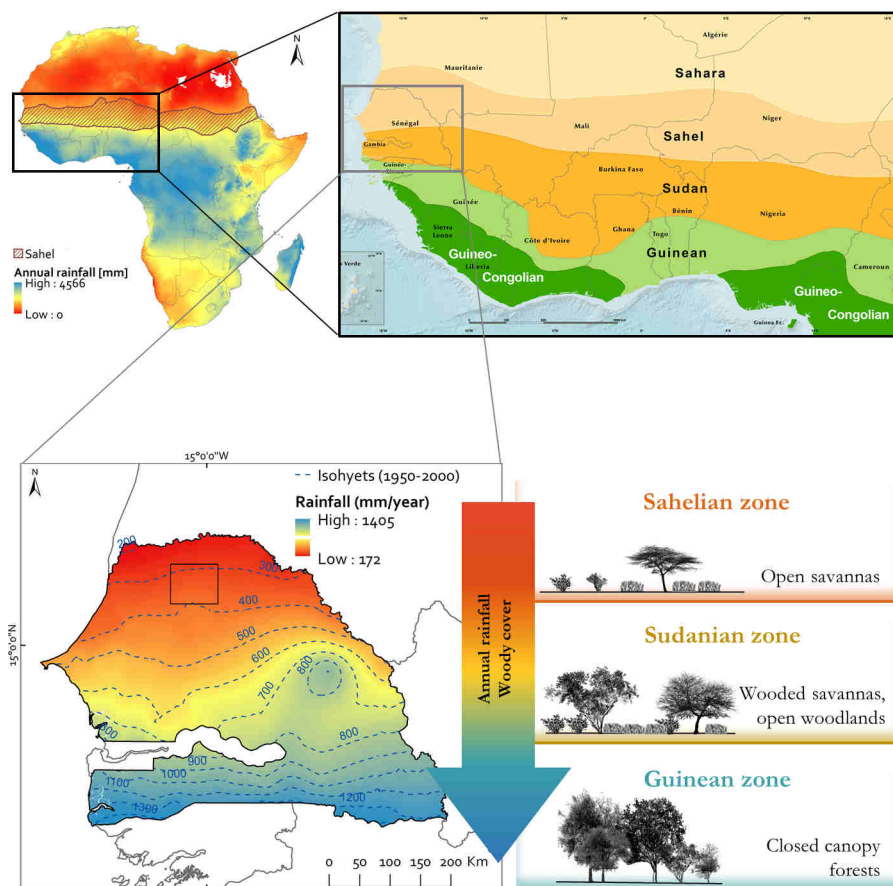


Figure 2.1 – Top-left: location of the Sahel in Africa and annual rainfall (no data in white) from WorldClim 2.0 (Fick and Hijmans, 2017). Top-right: zoom to West Africa and representation of the bioclimatic regions (map from CILSS, 2016). Bottom: vegetation types according to the rainfall gradient in Senegal with the study area framed in black.

The mean annual temperatures vary between 28-30°C, whereas the mean annual minimum and maximum are of 18-20°C and 35-38°C respectively, with January being the coldest month and May-June the hottest months (Hiernaux and Le Houérou, 2006; Le Houérou, 1989). The potential evapotranspiration is one of the most elevated in the world with 2800 to 3000 mm.year⁻¹ (Hiernaux and Le Houérou, 2006).

During the 1970s and 1980s, the Sahel was on the international research agenda as recurrent and severe droughts struck the area. Even if earlier in the 20th century, the region have known two other major drought episodes (during the 1910s and 1940s), the most intense was the one from 1970s to 1980s, with the driest years in 1972-73 and 1983-84 (Nicholson, 2013). In the early 1980s, rainfall fell to some 60% of the long-term mean (Nicholson, 2013). Nicholson *et al.* (2000) and L'Hote *et al.* (2002) stated that the drought still persists during the 1990s. Indeed, while being less dry than the two previous decades, this period stays the third driest decade of the 20th century (L'Hote *et al.*, 2002).

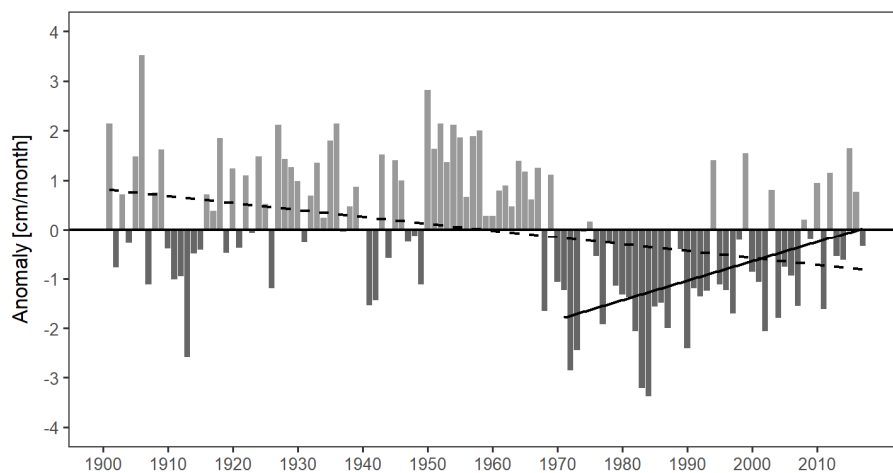


Figure 2.2 – Standardized rainfall anomalies in the Sahel region (10-20°N, 20°W-10°E) derived from station data, long-term trend since 1900 (dashed line) and short-term trend since 1970 (solid line). Reproduced from JISAO (Joint Institute for the Study of the Atmosphere and Ocean; Mitchell, 2018), with data from the Global Historical Climatology Network (GHCN).

There is no consensus about recent trends (after 1990) for the whole Sahel (Nicholson, 2013), but in the West African Sahel (from 10° to 15° W), the average rainfall between 1990 and 2007 is equivalent to the average of 1970-1989

(Nicholson, 2013). On the contrary in the Central Sahel (from 5° to 10° W), a recovery of rainfall occurred between 1990 and 2007 (Lebel and Ali, 2009). It is clear that the trends depend on the studied temporal scale with an increasing short-term trend since the 1970 but a decreasing one if we look back since 1900 (Figure 2.2).

2.1.3. Determinants of Sahelian vegetation

The typical plant formation encountered in the Sahel is an open savanna and comprises two layers: a sparse, perennial woody layer and a grass layer dominated by annual species (Hiernaux and Le Houérou, 2006; Le Houérou, 1989; Nicholson, 1995). White (1983) considers the Sahel as a transition zone, whereas the Sudanian zone is presented as a center of endemism. The number of plant species is of 1200 (woody and herbaceous) in the Sahel with less than 40 endemic species.

In his vegetation map of Africa, White (1983) distinguishes seven mapping units within the Sahel transition zone: (i) undifferentiated Sahelomontane vegetation; (ii) East African evergreen and semi-evergreen bushland and thicket; (iii) Sahel Acacia wooded grassland and Acacia deciduous bushland; (iv) Northern Sahel semi-desert grassland and shrubland; (v) mosaic of edaphic grassland and Acacia wooded grassland; (vi) mosaic of edaphic grassland and semi-aquatic vegetation; (vii) swamp and aquatic vegetation.

The type (iii), the Sahel wooded grassland, is the most widespread type occurring on sandy soils. The main species⁴ in the tree layer are: *Acacia tortilis* subsp. *raddiana* (Savi) Brenan, *Acacia laeta* R. Br. ex Benth., *Commiphora africana* (A. Rich.) Engl., *Balanites aegyptiaca*, *Boscia senegalensis* (Pers.) Lam. ex Poir., *Maerua crassifolia* Forssk. and *Leptadenia pyrotechnica* (Forssk.) Decne. and in the herbaceous layer, the annual species *Cenchrus biflorus* Roxb., *Schoenefeldia gracilis* Kunth, *Aristida stipoides* Lam., *Tragus racemosus* (L.) All. with sometimes perennial grasses such as *Andropogon* sp.

Vegetation is slightly different between the three eco-climatic subzones defined in section 2.1.1. In the Saharo-Sahelian zone, the woody species are mainly *Acacia laeta*, *Acacia hockii* De Wild., *Acacia ebrenbergiana* Hayne, *Leptadenia pyrotechnica*, *Capparis decidua* (Forssk.) Edgew. and *Salvadora persica* L.. The Sahelian zone mostly hosts spiny species such as *Acacia* sp., *Balanites aegyptiaca* and *Ziziphus*

⁴ See Appendix 1 for the full list of woody species mentioned in the document, their botanical authors and families.

mauritiana whereas in the Sudano-Sahelian zone, the Combretaceae family dominates, with *Sclerocarya birrea* (A. Rich.) Hochst., *Bombax costatum* Pellegr. & Vuillet, *Sterculia setigera* Del. and *Grewia bicolor* Juss. (Le Houérou, 1980d).

In the Sahelian and Sudanian zones of West Africa, the limiting factors for plant production are water and nutrients (phosphorus and nitrogen; Penning de Vries and Djiteye, 1982). From north to south, the most limiting factor changes, from water in the northern Sahel, to nutrients in the southern parts. The transition between these two types of limiting factors is located at approximately 250 mm.year⁻¹ of infiltrated water, which approximately corresponds to a mean annual rainfall of 300 mm (Breman and Kessler, 1995).

In addition to water and nutrients, the disturbance regime of grazing and fires also plays a role in determining savanna structure (Sankaran *et al.*, 2005). Grazing influences both herbaceous and woody vegetation through grass or leaves removal. The effects mostly depend on the season during which the browsing or grazing is occurring, the amount of biomass that is removed, and the plant capacity to endure grazing pressure (Breman and Kessler, 1995). Some species (grass or tree) tolerate a higher intensity of grazing than others and might even benefit from a moderate level of grazing (Miehe, 2002; Miehe *et al.*, 2010).

Besides woody biomass removal, livestock has additional effects on woody vegetation. For instance, they play an important role in the seed dispersal of some species (Breman and Kessler, 1995; Tybirk, 1991). They can also favor seedlings establishment through feces deposit, creating microhabitats favorable to seedlings of some species (Coughenour and Detling, 1986; Tybirk, 1991) and by reducing the competition with the herbaceous layer (Breman and Kessler, 1995). The positive impact on germination and establishment is however sometimes contested. Indeed, the seed germination capacity might be reduced by the passage to digestive tract (Danthu *et al.*, 1996). Moreover, the high nitrogen content in feces and the fact that the dung dries faster than the soil (because of its dark color) might be detrimental to the seedlings establishment (Tybirk, 1991; Wilson and Witkowski, 1998). Overall, the positive vs negative effects probably vary according to species, site and time (Miller and Coe, 1993).

Compared to the Sudanian zone, bush fires have a smaller impact on woody vegetation communities in the Sahel zone (Breman and Kessler, 1995). Low rainfall combined with grazing, limit the accumulation of biomass, thus reducing the fires occurrence. If the grass layer is patchy, it prevents the spread of fires (Breman and Kessler, 1995; Nielsen *et al.*, 2003). Sankaran *et al.* (2005) stated that woody cover of savanna is not impacted by fire in areas receiving less than

350 mm of annual rainfall. However, fire can still have negative effect on woody vegetation by killing small plants and regeneration (Bremen and Kessler, 1995; Poupon, 1980).

2.2. The Ferlo: sylvo-pastoral zone of Senegal

2.2.1. Study area

Tappan *et al.* (2004) divide Senegal in 13 ecoregions, essentially based on the boundaries created by the Direction de l'Aménagement du Territoire in 1984 with some adjustments (Figure 2.3, a). Ecoregions reflect the combination of biophysical components such as climate, geology, hydrology, soils and vegetation, and human factors (land use and settlements pattern). The sylvo-pastoral zone is composed of three ecoregions: the Northern Sandy Pastoral Region, the Southern Sandy Pastoral Region and the Ferruginous Pastoral Region.

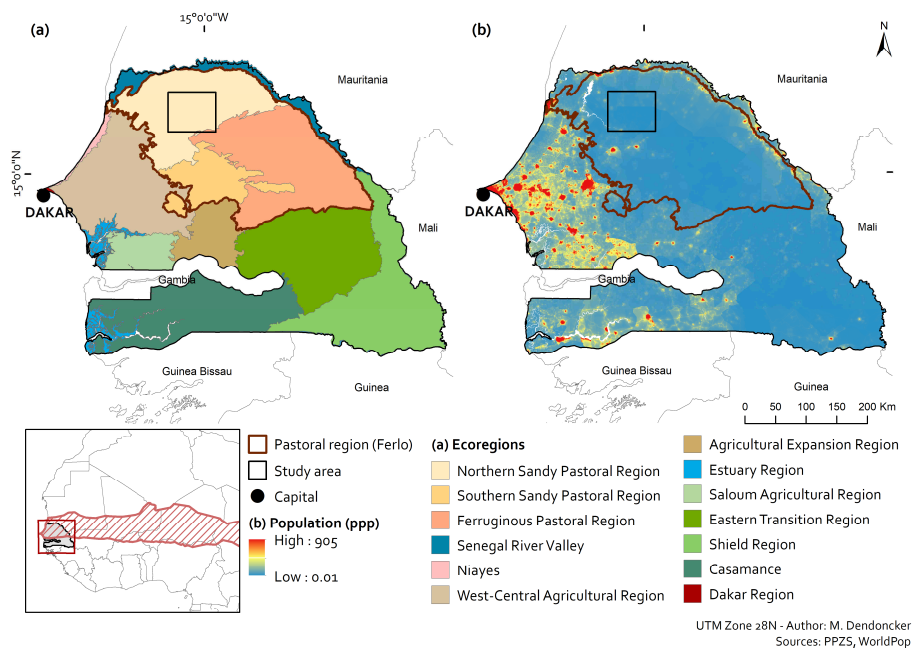


Figure 2.3 – Senegal (a) ecoregions as defined by Tappan *et al.* (2004); and (b) population density in 2015 (people per pixel, one pixel is a square of 100 m side; Tatem, 2017). The study area is framed in black. The hatched area in the bottom-left box represents the Sahel.

Our study area is located in the Northern Sandy Pastoral Region. This region presents a typical Sahelian climate with rainfall ranging from 300 to 500 mm.year⁻¹ during the 1960s and fell to 150-300 mm.year⁻¹ during the 1990s (Tappan *et al.*, 2004). The vegetation formation is an open savanna, with a relatively low woody cover (see Appendix 2, Figure A2.1).

Within the Northern Sandy pastoral region, the study area (68 km x 55 km) is centered on two deep wells: Widou Thiengoly (15.99° N, 15.32° W) and Tessékéré (15.85° N, 15.06° W, Figure 1.1)⁵. Physically, this zone is restricted to the east by the Ferruginous Pastoral Region, to the west and north by the Lake of Guiers and the Senegal River Valley, where irrigated agriculture is abundant. To the south, the isohyet of 400 mm.year⁻¹ serve as boundary. The study area is part of the “sylvo-pastoral reserve of the six deep wells”, which means that the land use is strictly reserved to sylvo-pastoralism with an agriculture activity nearly absent and restricted to a subsistence farming with rain-fed crops (Stancioff *et al.*, 1986). Several sylvo-pastoral reserves were created at the end of the 1980s to ensure the persistence of land dedicated to rearing (Cesaro *et al.*, 2010). The six deep wells that delimit the reserve are Tatki, Mbidi, Yaré Lao, Labgar, Amali and Widou Thiengoly (Figure 2.4).

The choice of Widou Thiengoly and Tessékéré was driven first, by the existence of historical data for this area and second, to benefit from the technical support of the installation of the forestry services at Widou. The most important one of these previous researches is perhaps the grazing trial carried out in Widou from 1981 to 2007 (Hiernaux, 2006; Miehe, 1994; Miehe, 2002; Miehe *et al.*, 2010). The main goal of this project was to study the influence of different grazing intensity on the herbaceous and wood stratum located on different topographical positions.

The evolution of woody vegetation for the second half of the 20th century in the different ecoregions of Senegal have been drawn by Tappan *et al.* (2004). In the Northern Sandy Pastoral Region (Figure 2.3), woody cover has decreased from 10-15% in 1942 and 1965, to 1-5% in 1994, with an exception for small depressions where the cover still reaches 10-40%. The greater water retention capacity of sandy soils, compared to ferruginous soils, has mitigated the effects of the great drought on woody vegetation. Brandt *et al.* (2014), Gonzalez (2001), Herrmann and Tappan (2013) and Vincke *et al.* (2010) also studied the long-term dynamics of woody vegetation in Senegal and Ferlo. In addition, Bakhoun

⁵ If this area should be modified for the computation of some indicators, it will be mentioned explicitly in the text.

(2013), Diouf (2011) and Ngom (2008) have also contributed to improve knowledge about the sylvo-pastoral resources in the Ferlo, their sustainable management, their dynamics and their uses by population.

2.2.2. Pastoralism: variable resources and mobility

Livestock farming is present in every department of Senegal with differences in the types of farming (extensive grazing, association with agriculture, etc.) and livestock density. In 2016, national census recorded 3 541 000 head of cattle, 6 678 000 sheep and 5 704 000 goats (Seye and Cissé, 2019).

While human population is relatively low inside the sylvo-pastoral area (Figure 2.3, b), the Ferlo remains the center of the Senegalese pastoralism (Cesaro *et al.*, 2010). Indeed, like the whole Sahel, the Ferlo receives too little precipitation to sustain permanent agriculture (Jahel *et al.*, 2020; White, 1983). In addition, fodder and water resources are highly variable from one year to another because of the high rainfall variability. Besides, from one season to another, the quality and the quantity of these resources are also submitted to changes. Pastoralism has been adopted as a strategy to cope with this resources variability.

In the Ferlo, the major part of the pastoralists belong to the Fulani people who live in semi-sedentary settlements. Pastoral families have to find a way to cope with the highly variable resources. Manoli *et al.* (2014) distinguish three means of livelihood security: the accumulation of “living” stock (i.e. herds, especially bovine herds), the diversification toward crops or non-farming activities and the mobility, which, in addition, is a way of maintaining the herds when local resources are lacking.

Water supply is the key factor that has ruled the annual mobility of pastoralists for decades. Prior to the 1950s, the Senegal River was the only permanent water point of the region. Temporary ponds, which are formed in small depressions during the rainy season, provided water for people and animals during the rainy season and during the first months of the dry season (up to November for the largest ones; Barral, 1982; see Appendix 2, Figures A2.5, A2.6 and A2.7). During this time of the year, Fulani herds grazed in the grasslands around the camps (see Appendix 2, Figure A2.3). Starting from the mid-dry season, they moved north, toward the Senegal River, or south, toward wetter regions to find grass and water. They returned inside the Ferlo at the beginning of the next rainy season. Therefore, the lands of the Ferlo were practically unoccupied during 6 months per year (Barral, 1982). The annual transhumance allowed to optimize the access

of livestock to water and the grazing quality of pastures. Thébaud and Batterbury (2001) stated that the pastoral mobility is a strategy that remains crucial because it allows the optimal use of dispersed, variable and heterogeneous resources.

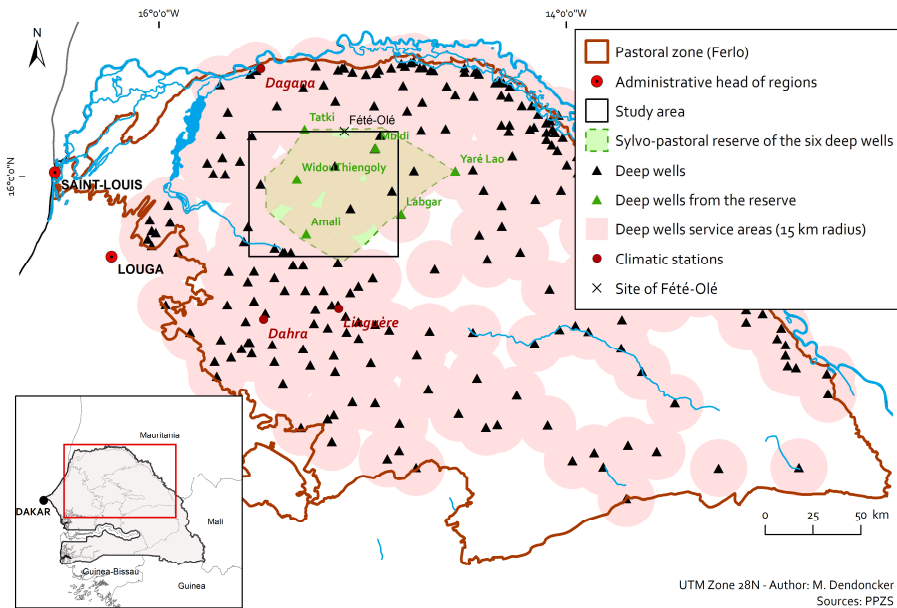


Figure 2.4 – The pastoral region (Ferlo), its deep wells and their theoretical service area (15 km radius) and location of the “sylvo-pastoral reserve of the six deep wells”. The study area is framed in black.

Starting 1950s, many deep wells were implanted in the Ferlo (Figure 2.4), following the discovery of the Maastrichtian aquifer (see Appendix 2, Figures A2.8 and A2.9). At the beginning, they were implanted 30 km apart from each other based on the statement that livestock could move up to 15 km in one day, so each deep well would have its “own” herds (Barral, 1982; Thébaud and Batterbury, 2001). However, the service area of a deep well is variable from one deep well to another, often depending on the pastures quality (Barral *et al.*, 1983). From 35 deep wells in 1957, this number reached more than 200 in 2000, including the numerous boreholes near the Senegal River Valley (Barral, 1982; Touré *et al.*, 2012).

This permanent access to water had several consequences. The more direct one is perhaps the decrease of the great seasonal transhumance pattern and a trend

toward sedentarization around the permanent water points (Touré *et al.*, 2012; Touré, 1990). Pastoral mobility remains but with different patterns and scales (Barral, 1982). The second consequence is that the number of animals raised considerably. From 1950 to 1983, cattle increased from 720.10^3 to 2250.10^3 , sheep from 506.10^3 to 2100.10^3 and goats from 747.10^3 to 1050.10^3 (Le Houérou, 1989). Finally, due to the greater number of animals and the attractiveness of the deep wells, grazing pressure on the vegetation increased.

2.2.3. Ecosystem services provided by woody vegetation

As the sylvo-pastoral land use is majoritarian in the Sahel and the Ferlo in particular, the importance of woody vegetation is most often emphasized through the provision of fodder and shadow (Le Houérou, 1980c; Le Houérou, 1980b) or through its effect on herbaceous productivity (Akpo *et al.*, 2005; Grouzis and Akpo, 2006; Le Houérou, 1980d). Yet, trees and shrubs provide many other provisioning, regulating and cultural services (Haines-Young and Potschin, 2018).

The value of some species can easily be grasped because of their direct uses by population for their fruits, their wood (as a source of energy or as material) or their uses in traditional medicine, as documented by ethnobotanical studies (Ayantunde *et al.*, 2009; Lykke *et al.*, 2004; Sop *et al.*, 2012; Wickens, 1980). A well-known example is the Arabic gum, produced by *Acacia senegal* and *Acacia seyal*. The gum can either supply a complement in the daily food or be sold on markets, bringing a complementary income to the households (e.g. Cervigni and Morris, 2015; FAO, 2010). A vast amount of literature is available regarding the ethnobotany, see for instance the review of Dounias (2000) who collected 400 references for Central and West Africa.

Regulating (nutrient cycling, water regulation, microclimate) and cultural (sacred trees, religious symbols) services are less studied probably because of their “indirect value”. A few examples are cited hereafter, even if sometimes the authors do not explicitly used the term “ecosystem services”. Bargués Tobella *et al.* (2014) outlined the positive influence of trees on the soil hydric properties in a semi-arid zone in Burkina. Grouzis and Akpo (1996) observed an enhancement of the hydric conditions under the shade of trees, along with a higher soil N content, in the Ferlo. Diallo *et al.* (2017) confirmed the positive effect of trees on nitrogen mineralization in the same region. To further illustrate the importance of the woody component of vegetation in the Sahel, we can cite the review of

Sinare and Gordon (2015) on both provisioning and regulating ES provided by woody vegetation in the Sahelian and Sudano-Sahelian zones (250-900 mm).

2.2.4. A brief overview of frequent woody species in the Ferlo

As some of the species are mentioned quite often in this work, we chose to present briefly 12 species that are frequently encountered inside our study area (Table 2.1). We provide a short description of their morphological aspect (growth form, leaves...) along with some elements of their ecology (soils and water requirements) and their main uses in West Africa or in the Ferlo. The phenology is valid for the Ferlo and the mean height is calculated after the fieldwork of 2015 (see section 3.3.1). Growth form expresses the extent of growth and the potential branching of the main-shoot axis. In this work, we will refer to three types of growth form: shrub, bush and tree. A shrub refers to a small woody plant with a height below 2 meters and multi-stemmed. A tree designates a woody plant taller than 5 to 6 meters, generally presenting a single trunk. A bush, or a dwarf tree as in Pérez-Harguindeguy *et al.* (2013), is the intermediary between a shrub and a tree. Its height is usually between 2 to 6 meters and it is often multi-stemmed.

Table 2.1 – Frequent woody species encountered in the Sandy Pastoral Region.

***Adansonia digitata* L.**

Malvaceae

Growth form: tree**Mean height:** 13.7 m**Description:** tree with a peculiar silhouette due to its large trunk and robust branches. The foliage is not very dense.**Ecology:** it grows on well-drained and deep soils. Mean annual rainfall requirement: 200-1000 mm.year⁻¹.**Uses:** the fruits and leaves are edible. The bark is used in traditional medicine and to make ropes.**References:** Arbonnier, 2009 ; Kindt *et al.*, 2013.

Photo: C. Vincke, February 2019

***Acacia senegal* (L.) Willd.**

Fabaceae

Growth form: bush or small tree**Mean height:** 5.2 m**Description:** thorny bush or small tree with open crown. Branches are very ramified and ascending. The spines are hook-shaped and measure 3 to 6 mm long. Deciduous, it bears leaves from July to January.**Ecology:** prefers sandy soils, drought resistant by an avoidance mechanism (leaf shedding). Mean annual rainfall requirement: 200-600 mm.year⁻¹.**Uses:** the species is well known for its sap, the Arabic gum, largely employed in pharmaceutical and cosmetic industries. In the Ferlo, the gum is eaten or sold on markets. The leaves and fruits are appreciated by livestock. Additional uses in traditional medicine, as firewood or construction wood.**References:** Arbonnier, 2009; Dendoncker, 2013; Gebrekirstos *et al.*, 2006; Poupon, 1979; Vassal, 1998.

Photo: M. Dendoncker, December 2017

***Acacia seyal* Del.**

Fabaceae

Growth form: tree

Mean height: 6.9 m

Description: thorny tree with a straight and cylindrical bole, open and spread crown. The spines are straight, disposed by pairs and measure up to 8 cm long. Deciduous, bears leaves between July and November.

Ecology: species encountered most often on downhill, near temporary ponds; on heavy clayed soils. Can cope with temporary flooding and episodic drought. Mean annual rainfall requirement: 200 to 1000 mm.year⁻¹.

Uses: as *Acacia senegal*, it produces Arabic gum. Provides fodder for livestock, and is used in traditional medicine and as firewood.

References: Arbonnier, 2009; Brandt *et al.*, 2016; Vassal, 1998.

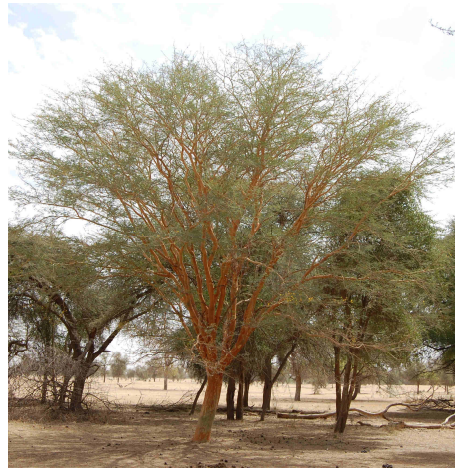


Photo: C. Vincke, February 2019

***Acacia tortilis* subsp. *raddiana* (Savi) Brenan**

Fabaceae

Growth form: tree

Mean height: 5.9 m

Description: spiny tree, the bole is cylindrical and the crown spreads like a parasol. The spines are straight and measure 5 to 10 cm. The species is semi-evergreen and bears leaves during 11 to 12 months.

Ecology: prefers sandy soils, drought resistant thanks to an avoidance mechanism (leaves shedding) and a tolerance mechanism (low hydric potential). Mean annual rainfall requirement: 200 to 1500 mm.year⁻¹.

Uses: the leaves and pods provides food for livestock, the wood is used as firewood and construction wood.

References: Arbonnier, 2009; Gebrekirstos *et al.*, 2006; Grouzis and Le Floch, 2003.



Photo: M. Dendoncker, August 2015

***Balanites aegyptiaca* (L.) Del.**Zygophyllaceae

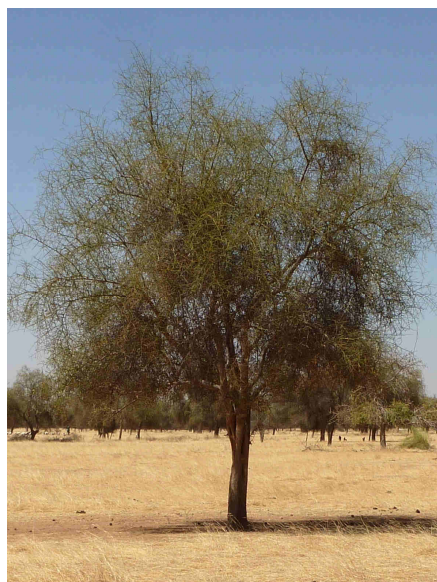
Growth form: tree**Mean height:** 5.7 m**Description:** evergreen, thorny tree with a spherical crown, flat or irregular. Its shape is peculiar because of its branches that are supple and falling down. The spines are straight and measure 8 to 10 cm long.**Ecology:** grows well on any kind of soils and in any topographical position. Drought resistant because of its evergreen foliage and its low water potential. Mean annual rainfall requirement: 200 to 900 mm.year⁻¹.**Uses:** the wood is used as construction wood, it is insect resistant. The fruits are edible and are often sold on local markets. The fruits and leaves are eaten by goats. Also used in traditional medicine.**References:** Arbonnier, 2009; Dendoncker, 2013; Gebrekirstos *et al.*, 2006; Le Hou  rou, 1980c.

Photo: M. Dendoncker, April 2016

***Boscia senegalensis* (Pers.) Lam. ex Poir.**Capparaceae

Growth from: shrub, in rare case, bush**Mean height:** 1.5 m**Description:** evergreen shrub with a rounded crown, dense foliage, with strong leaves.**Ecology:** encountered on dry sites, on sandy or lateritic and rocky soils.**Uses:** the fruits are eaten in case of shortage; the wood is used to make stakes. Cattle consume the leaves mostly at the end of the dry season.**References:** Arbonnier, 2009; Dendoncker, 2013.Photo: M. Dendoncker, August 2015

***Calotropis procera* (Ait.) Ait. f.**

Apocynaceae

Growth form: shrub

Mean height: 2.1 m

Description: evergreen shrub, with an irregular crown formed by a small amount of branches. The leaves are tall and rather succulent.

Ecology: most often encountered on sandy soils but can also grow in wetter sites on degraded soils.

Uses: the wood serves to build fences and stakes. The dried leaves and flowers are eaten by sheep and goats.

References: Arbonnier, 2009; Dendoncker, 2013.



Photo: D. Fecherolle, August 2015

***Combretum glutinosum* Perr. ex DC.**

Combretaceae

Growth form: tree

Mean height: 7.4 m

Description: semi-evergreen tree, with a tortuous bole and an open rounded crown.

Ecology: grows on any type of soils, drought resistant. Mean annual rainfall requirement: 200-900 mm.year⁻¹.

Uses: the wood is used in construction, firewood. The leaves are eaten by livestock. Also used in traditional medicine.

References: Arbonnier, 2009.



Photo: M. Dendoncker, December 2017

Grewia bicolor Juss.Malvaceae

Growth form: bush**Mean height:** 4.6 m**Description:** deciduous bush that bears leaves from mid-July to March.**Ecology:** encountered inside small depressions, often near temporary ponds. Often on sandy soils but also on rocky lateritic soils. Mean annual rainfall requirement: 200-800 mm.year⁻¹.**Uses:** used in traditional medicine. The young leaves are eaten by livestock.**References:** Arbonnier, 2009; Kindt *et al.*, 2013; Le Houérou, 1980c; Poupon and Bille, 1974.

Photo: D. Fecherolle, August 2015

Guiera senegalensis J. F. Gmel.Combretaceae

Growth form: bush**Mean height:** 4.1 m**Description:** semi-evergreen (bears leaves from July to April) bush with irregular crown.**Ecology:** grows on depleted or leached out sandy soils.**Uses:** the leaves and fruits are eaten by livestock, the wood is used as firewood and construction wood. Also used in traditional medicine.**References:** Arbonnier, 2009; Bille, 1977; De Bie *et al.*, 1998; Poupon, 1979; Poupon and Bille, 1974.Photo: C. Vincke, February 2019

***Sclerocarya birrea* (A. Rich.) Hochst.**

Anacardiaceae

Growth form: tree

Mean height: 9 m

Description: tree with a rounded and dense crown. Deciduous, bears leaves from mid-May to January. The tree is easily recognizable by its bark.

Ecology: grows on sandy soils. Mean annual rainfall requirement: 400-1200 mm.year⁻¹.

Uses: the leaves and bark are eaten by livestock. The wood is used as firewood and to make tools. Also used in traditional medicine.

References: Arbonnier, 2009; Poupon, 1979; Poupon and Bille, 1974.

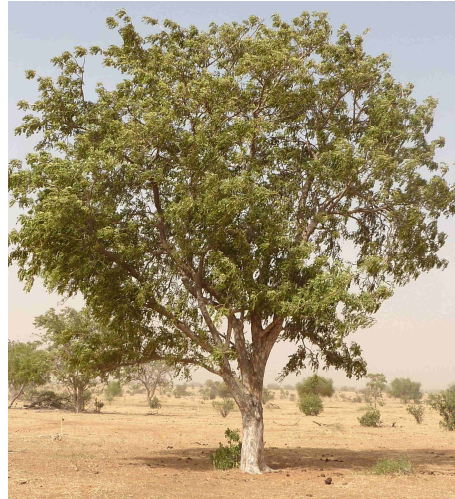


Photo: M. Dendoncker, December 2017

***Ziziphus mauritiana* Lam.**

Rhamnaceae

Growth form: tree

Mean height: 6 m

Description: small thorny tree with rounded crown and falling down branches. The spines are short and hook-shaped. Deciduous, bears leaves between June and January.

Ecology: grows on sandy or rocky soils, often near a temporary pond. Mean annual rainfall requirement: 120-2200 mm.year⁻¹

Uses: The fruits and leaves are edible. The leaves are eaten by sheep and goats. The wood is used as firewood, construction wood. Also used in traditional medicine.

References: Arbonnier, 2009; Dendoncker, 2013; Kindt *et al.*, 2013; Poupon, 1979; Poupon and Bille, 1974.



Photo: D. Fecherolle, August 2015

2.3. Persistence and resilience: what are we talking about?

An important aspect of this research is the focus on the woody vegetation persistence through years. Persistence is often associated with the resilience concept and other associated terms. They are widely used in ecology and their meaning often vary from one author to another. We intend to give first an overview of these concepts and second to clarify how they are to be understood in this research.

2.3.1. Concepts and definitions

The resilience concept was originally introduced by Holling (1973), who defines it as a system property that “determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist”. The concept and its field of application has evolved and today, resilience definitions are numerous in the literature so that the concept can be tricky to capture. Still, several authors distinguish two main facets of the resilience (Brand and Jax, 2007; Carpenter *et al.*, 2001; Holling, 1996; Miller *et al.*, 2010). The first definition focuses on the *recovery after a disturbance* and the rate at which this recovery happens, and can be referred as “engineering resilience” (Brand and Jax, 2007; Holling, 1996). The second definition focuses on how the system can *persist under disturbances*, without changing function. This is close to the original definition proposed by Holling (1973) and corresponds to the “ecological resilience” (Brand and Jax, 2007; Holling, 1996).

Miller *et al.* (2010) explain a further distinction between “specified resilience” and “general resilience”. The specified resilience refers to the “resilience of what to what” as in Carpenter *et al.* (2001). The study of a particular function (e.g. an ecosystem service) facing a particular disturbance (e.g. grazing, fire) and the question of knowing if the variables will cross a threshold and shift to another state. The general resilience considers all the aspects of the system, where the disturbances are unspecified and can be unknown. Brand and Jax (2007) proposed a typology for the multiple definitions of the resilience of the second category.

The stability concept is tightly related to resilience. It is also subject to confusion because of its multiple definitions and its origin. Indeed, the stability concept comes from the field of physics and mathematics where it is applied to simple

dynamic systems, which are not the case of ecological systems (Grimm and Wissel, 1997). Grimm and Wissel (1997) reviewed the multiple definitions and terms of the stability concept and identified three fundamentally different properties: (1) constancy, “staying essentially unchanged”; (2) resilience, “returning to the reference state after a temporary disturbance”; and (3) persistence, “persistence through time of an ecological system”.

In addition, Grimm and Wissel (1997) add three aspects belonging to the first two properties that are often cited in literature. First, the resistance, an aspect of property 1, defined as “staying essentially unchanged despite the presence of disturbances”. Second, the elasticity, “speed of return to the reference state (or dynamic) after a temporary disturbance”. Third, the domain of attraction, “the whole of states from which the reference state (or dynamic) can be reached again after a temporary disturbance”. Elasticity and domain of attraction are aspects of property 2 (resilience). We note that the second property of stability (the resilience property) can be related to the “engineering resilience” defined above and that the constancy property (through the resistance aspect) is close to the “ecological resilience”.

As one of the sources of confusion is the multiplicity of ecological situations, the same authors further highlight the necessity to describe and define any ecological situation for which a stability assessment is undertaken. Their ecological checklist includes six points, that together characterize the validity domain of the research: the level of description, the variable of interest, the reference state and the reference dynamic, the disturbance, the spatial scale, and the temporal scale, even if this scale is not part of the resilience definition (Grimm and Wissel, 1997).

As resilience is about how a system responds to stresses and disturbances, it is equally important to clarify these terms as well, given the fact that several definitions exist. Grime (1977) stated that the factors that potentially hindered plant growth can be classified in two groups: stress, which is a condition that will limit the biomass production (e.g. light or water deficit), and disturbance, which implies a partial or complete destruction of biomass (e.g. grazing). Gallopin (2006) has another definition and considers a stress as a continuing or gradual increasing pressure inside the normal domain of variability of the system in which the system is usually functioning. Stresses are often internal to the systems. Disturbance is a major pressure peak outside the normal domain of variability of the system and usually comes from outside the system (external factor). In this work, we will use the term “disturbance” (or “pressure” as a synonym), relating to the definition of disturbance of Mouillot *et al.* (2013): “any event, natural or

human driven, that causes temporary and localized shifts in demographic rates”. Indeed, we are interested in factors that are susceptible of influencing the vegetation state, whatever their origin or whatever their effect on biomass.

2.3.2. Resilience and persistence in this research

The term “resilience” is used in this work as a conceptual framework used to position woody vegetation dynamics within a context of a changing environment and to study how these changes will potentially affect this vegetation (i.e. what is the trajectory of the vegetation).

Compared to the two main facets of the resilience, this research focuses on the ecological resilience (or the persistence and constancy properties of Grimm and Wissel, 1997). Moreover, as we are studying one particular component (i.e. woody vegetation) in face of defined pressures, this corresponds to the “specified resilience”. Furthermore, as we aim to consider the woody vegetation within the context of a pastoralist land use an appropriate definition would be the following: “the underlying capacity of an ecosystem to maintain desired ecosystem services in the face of a fluctuating environment and human use” (Brand and Jax, 2007).

The notion of “desired ES” would therefore be those who underpin sylvo-pastoralism (e.g. fodder provision, maintenance of soil fertility, see 2.2.3). In order to assess if these ES will still be provided by woody vegetation in the future, we will focus on some persistence indicators that are of particular importance to (i) evaluate the future trajectory of woody vegetation (regeneration, ratio trees vs shrubs) and (ii) to better understand the effect of woody vegetation on two ecosystem functions (functional diversity).

2.4. Functional diversity

2.4.1. A functional approach of communities

Ecologists wanted to link the ecosystem functioning to biodiversity since long. At the origin, there is the hypothesis that a higher taxonomic biodiversity (e.g. a high species richness) would enhance the ecosystem processes or its ecological resilience. According to Tilman (2001), it was Darwin who first suggested a link between biodiversity and productivity by stating that the increase in species richness of pastures would enhance their primary productivity.

More recently, another aspect of biodiversity, functional diversity (FD), has proved to be a better predictor of ecosystem functions and ecosystem resilience (Villéger *et al.*, 2008). Functional diversity is the biodiversity component that target what the species actually “do” in ecosystems and is, therefore, the link between the scale of organisms and ecosystems (Petchey and Gaston, 2006). Several definitions of FD exist, with perhaps the most common being the one of Tilman (2001), who defined it as “the value and range of the functional traits of the organisms in a given ecosystem” (Figure 2.5).

Garnier and Navas (2012) stated that a trait-based approach should allow solving three issues. First, it should help us to understand how the organisms function and what are their relationships to the environment (biotic and abiotic factors). Second, it should clarify the rules that lead to the communities’ assemblages (see e.g. Mouchet *et al.*, 2010). Third, it should bring some light on the links between the organisms functioning, the ecosystem functioning and the ecosystem services. Functional diversity has thus a role to play in the ecosystem resilience. The specific links between FD and resilience will be developed in Chapter 6.

Measuring functional diversity is therefore about measuring the diversity of functional traits. A trait is defined as “any morphological, physiological, phenological feature measurable at the individual level (...) without reference to the environment or any other level of organization” whereas functional traits point to the traits “which impact fitness indirectly via their effects on growth, reproduction and survival” (Violle *et al.*, 2007). Nock *et al.* (2016) also include in the definition of functional traits, the traits that have an effect on ecosystem processes, hence “traits (...) that influence how the organisms respond to the environment and/or their effect on ecosystem properties”.

In this work, we use the term “trait” as a shortcut for functional traits. (Functional) traits can be nominal (or categorical; e.g. growth form) or continuous (e.g. leaf size). The value or modality taken by a trait is called an attribute (Violle *et al.*, 2007). For instance, the categories “shrub”, “bush”, and “tree” are some attributes that can be taken by species to characterize their growth form.

It is important to precise two points. First, the attributes shown by one species for a trait can change along *environmental gradient*. An example of this variation is the growth form of *Acacia senegal* along a water availability gradient. Indeed, individuals of this species are often small trees, but individuals growing in driest sites can present themselves as bushes (Gebrekirstos *et al.*, 2006). Second, the assessment of attributes is often performed at the *population scale* (by taking the

average of the attributes presented by the different individuals composing this population) for a particular spatio-temporal scale (Garnier and Navas, 2012; Violle *et al.*, 2007). This lead to the consequence that “there is not a single-trait attribute for any particular species” (Garnier and Navas, 2012).

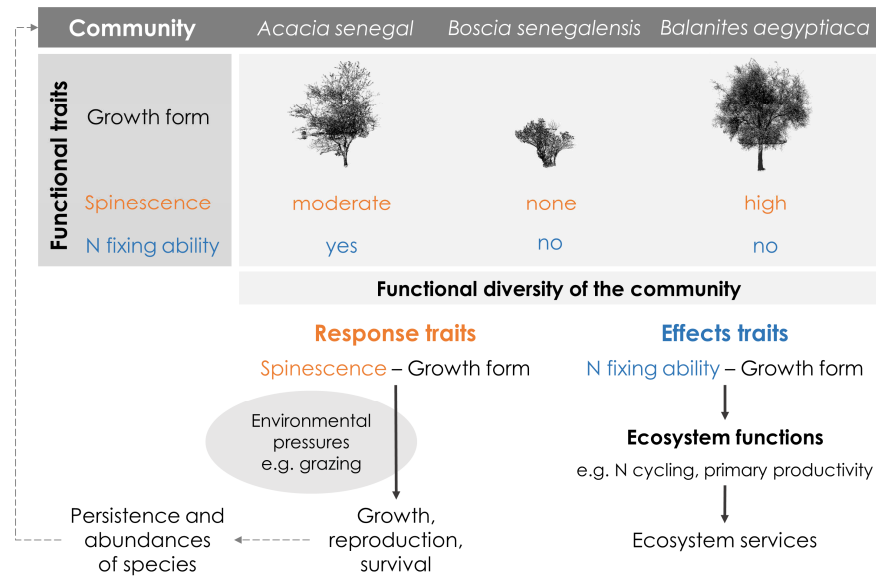


Figure 2.5 – Example of a community with three species and considering three functional traits (growth form, spinescence, N fixing ability). Two of these traits are response traits: growth form and spinescence; and two are effects traits: growth form and N fixing ability. The response traits influence how the species will react in face of a pressure. Subsequently, the species abundances in the community can be affected (dashed grey arrow). The effects traits express how the species affect the ecosystem functions and ecosystem services. The functional diversity of this community is represented by the greyish rectangle, and therefore comprises the different modalities (attributes/traits values) for the three traits taken by the three species.

Functional traits can be classified according to whether they affect the ecosystem processes or whether they influence the species responses to their environment. Traits that have an influence on ecosystem properties and possibly on the ES derived from ecosystem, are called “effects traits”. Traits that influence how the species will grow in a habitat and how they behave in face of an environmental factor are called “response traits”. It is important to note that those categories are not mutually exclusive, as a functional trait can be a response trait and an effect trait at the same time (Nock *et al.*, 2016).

For instance, the capacity of a species to fix nitrogen (N fixing ability) is an effect trait, as it influences the process of N cycling in the ecosystem (Figure 2.5). The presence and the amount of spines (spinescence) that a species exhibits is a response trait. Indeed, species respond differently to grazing according to whether they have spines or not. Growth form however, is simultaneously an effect trait through its effect on primary productivity (biomass) and a response trait, as herbivores have a more or less easy access to foliage according to the plant height.

Traits can also be referred as “hard traits” if the trait is directly related to a plant function. Traits that are less related to a particular function are called “soft traits”. They are used as proxy for hard traits because their measurement is easier (origin of the dichotomy: Hodgson *et al.*, 1999). More details can be found in Lavorel and Garnier (2002); Nock *et al.* (2016) and Violle *et al.* (2007).

Table 2.2 gives three examples of soft traits and their corresponding hard traits, in relation to the response to one pressure (fire) and to the effect on one ecosystem function (primary productivity). The seed mass is a soft trait that influences the organism response to fire through the mechanism of regeneration. Three hard traits are directly related to this mechanism: fecundity, seedling establishment, dispersal. Table 2.2 also shows that traits can be effect and response traits at the same time, like the growth form and the specific leaf area.

Table 2.2 – Examples of soft traits and their corresponding mechanism and hard traits for an environmental response (fire) and an ecosystem effect (primary productivity).

Extracted from Lavorel and Garnier (2002).

Soft trait	Mechanism and corresponding hard traits	
	Response to fire	Effect on primary productivity
Growth form	Avoidance: plant/bud height (physical escape), phenology (temporal escape) Regeneration: strategy (resprout vs. seed)	C stock: standing biomass Resource capture: standing biomass Growth: growth rate
Specific leaf area (SLA)	Tolerance: resprout relative growth rate Regeneration: seedling relative growth rate	C fixation: leaf instantaneous photosynthetic rate
Seed mass	Regeneration: fecundity, seedling establishment, dispersal	/

2.4.2. Functional diversity components and related indices

As the interest in the FD concept increased, the question of how to measure the functional diversity was raised. First, it is important to note that, like for biodiversity, functional diversity can be decomposed in several components and that several metrics or indices exist to quantify either the FD concept in its whole, and/or one of its components. The two notions, FD components and FD indices should not be confused.

Mason *et al.* (2005) distinguish three complementary components (Figure 2.6) in functional diversity that, taken together, describe the distribution of the species and their abundances in the functional space (i.e. the multidimensional space composed of axes that represent functional features; Mouchet *et al.*, 2010). The first component is the functional richness, that is, “the amount of niche space filled by species in the community” (Mason *et al.*, 2005). This component is independent of the species abundances, as a portion of space that is occupied will be so, even if there is only one individual of the species. The second component is the functional evenness, or “the evenness of abundance distribution in filled niche space” (Mason *et al.*, 2005), that is the repartition of abundances between the different trait values. The third component, the functional divergence, represents “the degree to which abundance distribution in niche space maximizes divergence in functional characters within the community” (Mason *et al.*, 2005). To simplify, it is the same as to look how the species abundances are spread on the range of traits values. A highly divergent community is a community in which there are more individuals belonging to species that present extreme traits values.

Petchey and Gaston (2006) classified the functional diversity measures in two categories: the discontinuous measures and the continuous measures. The discontinuous measures are equivalent to gather species that have similar effect in functional groups and to take the number of groups as a FD measure. While it can be rather straightforward and easy when dealing with categorical traits and functions like N-fixers vs non N-fixers, it is more complex when it comes to continuous traits. In that case, classes are to be created from the continuous measures (e.g. leaf area classified in “small”, “medium”, and “large”) which implies making decisions about the breaks between classes. The disadvantage of making groups is that first, we overlook the differences inside a group (e.g. leaf area varies between species classified in the “small” category), and second, it implies making arbitrary decisions about which amount of difference is sufficient

to classify one species in another group. The continuous measures place the species inside a n -dimensions traits space, n being the number of studied traits, and assess their positions inside this space.

Among the continuous measures, several metrics exist for the three FD components. We present here the ones used in this work. Indices for functional richness, evenness and divergence (FRic, FEve, FDiv) have been first proposed by Mason *et al.* (2005) for single-trait approaches. The fact that these indices bear the same name that the components they mean to measure, can bring confusion, but it is important to separate the FD components from the indices. Villéger *et al.* (2008) presented an upscaling to multiple-traits approaches of these three indices via the positioning of species in a multidimensional space. Finally, Laliberté and Legendre (2010) updated the same three indices by describing a distance-based framework to measure them in a multidimensional traits space. This framework is based in the computation of a Principal Coordinates Analyses⁶ on the species traits and will be further explained in Chapter 6. Their indices are valid for any number of traits and whatever their types (continuous, categorical, and ordinal) and can be easily computed with the “FD” R package (Laliberté *et al.*, 2014; see Appendix 4 for the mathematical formulas of the indices).

In addition to these three indices, two other indices measuring two other components of FD are available in this package and will be used in this work. The first one, the CWM (community-level weighted means of trait values) measures the concept of functional identity (Figure 2.6). Moullot *et al.* (2011) define functional identity as the “the biomass-weighted mean trait value for a community” and identify it as a key component in explaining the multifunctionality of ecosystem. The CWM index is, for each trait, “the mean of values present in the community weighted by the relative abundance of taxa bearing each value” (Lavorel *et al.*, 2008). The second index, is the functional dispersion, FDis, which assesses the spread of the species compared to the center of the functional space and it is defined by the “mean distance of individual species to the centroid of all species in the community” (Laliberté and Legendre, 2010). In a single-trait approach, this would be measured for instance by the variance or standard deviation of the mean trait. FDis is not explicitly related to one of the three primary components of FD.

Among the multiple indices, choosing one that is appropriate for a specific research can be difficult. While Petchey and Gaston (2006) stated that there is not one unique good way to measure FD, Mouchet *et al.* (2010) demonstrated

⁶ A summary of the multivariate analyses used in this work is available in Appendix 3.

that the three FD components (richness, evenness and divergence) could not be captured in one single index. As studying the links between FD and ecosystem functioning requires the integration of these three components, Mouchet *et al.* (2010) therefore suggest to use a combination of indices, one for each of the three components.

For instance, if we imagine two fictive communities (C1 and C2), we can represent the distribution of the species abundances on one axis (y-axis) and consider the repartition of the values for one trait, e.g. the leaf size, on the x-axis (Figure 2.6). The x-axis therefore represents the functional space. The functional richness (panel a) is the range of the different leaf sizes that are represented in the two communities, which corresponds on the graph, to the width of the curves. C2 has a higher functional richness as it contains species with leaf size ranging from 1 to 12 cm² (the numbers are given as example) whereas C1 has species with leaf area from 2 to 6 cm². The functional evenness (panel b) of C1 is greater than C2. Indeed, C1 has the same species abundances for each leaf size value whereas C2 has more individuals belonging to species having larger leaves than smaller leaves. The functional divergence (panel c), i.e. the repartition of the abundances regarding the extremities of the x-axis, is greater for C2 than for C1. C1 has many individuals belonging to species with medium leaf size whereas C2 has many individuals belonging to species with very high and very low leaf size and no species presenting medium size. The functional dispersion (panel d) of C1 is lower than C2 because C1 has less individuals belonging to species with extremes leaf size (very small and very large leaves) compared to the mean leaf size. The functional identity of C1 is lower than C2 because the weighted mean of the leaf size of all the individuals in the community (represented by the value on the x-axis pointed by the vertical line on the graph) is lower than C2 (for instance the weighted mean of C1 is 2 cm² and 8 cm² for C2).

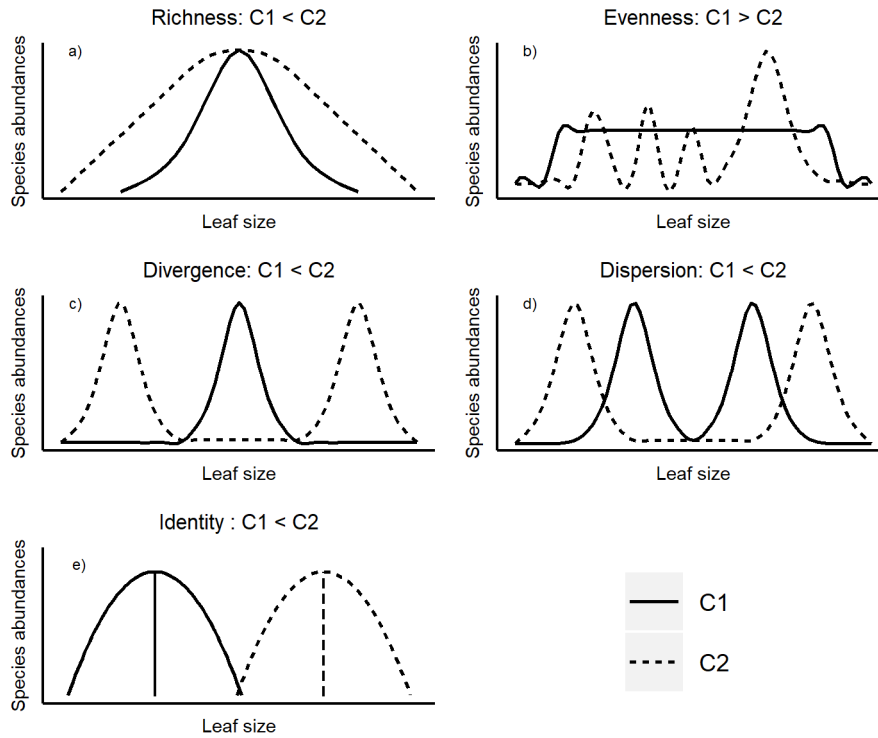


Figure 2.6 – Functional diversity components (functional dispersion is considered as a component on its own) for two theoretical communities, C1 (solid line) and C2 (dashed line). The two communities are not the same from panel a to e, and they do not necessarily host the same number of species. The x-axis represents the range of attributes taken by one single functional trait (here, the leaf size). The y-axis represents the abundances of the species within the communities. a) Functional richness, illustrated by the width of the curve on the x-axis. C1 has a smaller richness than C2. b) Functional evenness, illustrated by the distribution of the abundances. c) Functional divergence illustrated by the repartition of the abundances regarding the extremities of the functional space. d) Functional dispersion illustrated by the distribution of the abundances regarding the middle of the curve. e) Functional identity, the values pointed on x-axis by vertical lines. From b to e, the two communities present the same functional richness (the width of the two curves are identical). Adapted from Taugourdeau (2014).

Chapter 3

Materials and methods

— *Outline* —

As stated in Chapter 1, this thesis relies on multiple disciplinary angles, each of them needing a particular methodology. This chapter serves as foundation for the whole document as we present some of the methodologies that underlie the next chapters. Detailed and specific methodologies will be explained in the corresponding chapters. First, we explain how the different disciplines articulated themselves to achieve the goals presented in Chapter 1. Second, we describe the study area inside the Ferlo in terms of soils, vegetation, climate and population. Third, we present each of the datasets that are used in this research. Finally, we summarize the integration of the different datasets in the four following chapters. A particularity of this chapter is that it includes some content that could be assimilated to results (e.g. climate data analysis and the Fulani settlements recording). We choose to present them here, as they are integral parts of the study area description and constitute necessary background to frame this work.

3.1. General methodology: a multidisciplinary approach within the field of ecology

Long-term trends of woody vegetation can be assessed at different spatial scales (local, regional), with various indicators (cover, density, species composition) that are acquired through different methodologies (field inventory or remote sensing for instance). Each of these approaches has its advantages and disadvantages. More and more studies have integrated a multidisciplinary approach to study Sahelian vegetation (e.g. Brandt *et al.*, 2014; Gonzalez, 2001; Hänke *et al.*, 2016; Herrmann and Tappan, 2013)

We chose to rely on different methodologies and to use multiple datasets in order to get the broadest and complete view of the changes affecting vegetation. Among the disciplinary angles that will be mobilized, we can cite forestry (field inventory), ecology (trait-based approach), and geomatics (remote sensing). We aim to take advantage of each field area and to compensate the down sides of the different methodologies. We distinguish three types of datasets: field dataset, remote sensing dataset and species traits dataset, each of them is detailed in section 3.3.

Field inventories describe the current state of vegetation on the field and allow an approach at the species level. One disadvantage of this field approach is that it is time consuming and requires a lot of working force. The consequence is that the ratio “time on the field/inventoried surface” is not high. For instance, based on our field experience of 2015, the average number of plots inventoried per day is five, which corresponds to a surface of 2.25 ha. For a plot located on top with few individuals, the required time to complete the inventory can be very low (less than an hour), with the help of 2 to 3 workers. However, plots located in depressions can take three hours to inventory, with hundreds of individuals to record and measure. Another disadvantage, tough not inherent to all field study, is the lack of geotagged historical data. The vegetation (herbaceous and ligneous) of the Ferlo has been intensively studied during the 1970s and the 1980s, with, among others, the works of H. Poupon, J.C. Bille and J. Valenza (e.g. Bille, 1973; Poupon, 1980; Valenza and Diallo, 1972b). Unfortunately, their field observations cannot be located with accuracy, as these studies date from the time before the availability of GPS. Two datasets contain field data: the field inventory of 2015-2017 carried out in the frame of this work (see section 3.3.1) and a vegetation database that gathers hundreds of botanical surveys conducted in northern tropical Africa (see section 3.3.2).

Data from field inventory are mostly tools to study the spatial variability of current woody vegetation in Chapter 4 (specific objective 1). Part of the inventory data are also integrated in Chapter 5 (temporal dynamics, specific objective 2) as a validation set for satellite imagery. Finally, they are also used in the trait-based approach developed in Chapter 6 (specific objective 3). The historical inventory data from a vegetation database are part of Chapter 5 as a source of botanical composition before and during the great drought.

Using Earth observation datasets (i.e. satellite or aerial photos, see section 3.3.3) has the advantage to allow the study of large area at lower cost and the possibility to have repeated observations through time. However, the output indicators are usually less precise than field measurements, particularly in case of multiple vegetation layers composed by individuals with different height and with overlapping crown (bushes beyond trees). Besides, it is quite often impossible to distinguish the species. Some satellites images (e.g. Corona) and aerial photos bring insights regarding the temporal dynamics of vegetation. However, these historical data can be difficult to interpret and their processing can be time consuming due to the differences in spatial resolution and/or the need for a georeferencing. Satellite imagery and aerial photos are used for the assessment of woody vegetation changes in Chapter 5 (specific objective 2).

The field area of functional ecology is mobilized to link the past and current species composition to the ecosystem functioning and to the vegetation response to three pressures (specific objective 3). The trait-based approach developed in Chapter 6, relies on the gathering of traits data from a literature review (see section 3.3.4).

3.2. Bio-physical, climatic and human context of the study area

3.2.1. Geomorphology, soils and vegetation

The major landform of the study area, macrorelief as called in this work, is composed of an alternation of sand dunes and plains. The dunes, which were formed 15 000 to 20 000 years ago, are oriented in a northeast-southwest direction. They measure 10 to 30 meters high, 20 to 50 km long and 0.5 to 5 km wide. Longitudinal plains of 1 to 5 km wide separate the dunes (Le Houérou, 1989). During the rainy season, temporary ponds form inside these plains as the soils contain more clay. Bille *et al.* (1972) distinguish three types of landscape

physiognomy (see Appendix 5). Our study area belongs to the category of “large dunal system”.

While soils are mainly sandy, they slightly change with the landform. Ferruginous tropical soils (French classification) are found on the dunes whereas in the plains, subarid red and brown red soils are predominant (Figure 3.1, Le Houérou, 1989). These two types of soils have a low organic matter content but slightly higher in the subarid brown soils (1 to 4%) than in the ferruginous tropical soils (0.2 – 0.5%; Charreau and Fauck, 1965; Khouma, 2002). According to the World Reference Base for Soil Resources (WRB), these two types correspond to the Ferralic arenosols and Brunic arenosols, and belong to the group of “relatively very homogenous sands and young soils that have limited or poor profile development” (Jones *et al.*, 2013). Ferralic arenosols are sandy soils that are intensely weathered and with a high iron content. The qualifier “ferralic” means that soils have “a horizon within 100 cm of the soil surface where the clay fraction is dominated by low-activity clays and the silt and sand fractions by highly resistant minerals, such as (hydr)oxides of Fe, Al, Mn and Ti” (Jones *et al.*, 2013). Brunic arenosols are sandy soils with a leached and reddish horizon. The qualifier “brunic” refers to soils with “a layer starting within 50 cm of the soil surface, at least 15 cm thick, which meets certain alteration criteria of the cambic horizon but lacks the cambic texture criteria”. Both types are vulnerable to wind erosion in the absence of vegetation (Jones *et al.*, 2013).

In the frame of a study to map Senegal resources, vegetation was classified in 25 major types (Stancioff *et al.*, 1986). The study area is covered with “bushy pseudo-steppes”, plateau and peneplain formations, the units Ac4 and Acm5 (Figure 3.1). Woody vegetation of the unit Ac4 is composed of *Sclerocarya birrea* and *Adansonia digitata* in the tree layer and *Balanites aegyptiaca*, *Guiera senegalensis* and *Boscia senegalensis* in the bush layer. Associated species are *Acacia senegal*, *Combretum glutinosum*, *Calotropis procera* and *Terminalia avicennioides* Guill. et Perr.. The major herbaceous species are *Eragrostis tremula* (Lam.) Hochst. ex Steud., *Dactyloctenium aegyptium* (L.) Willd., *Zornia glochidiata* Rchb. ex DC., and *Alysicarpus ovalifolius* (Schumach. & Thonn.) J. Léonard. In the interdunal plains, the tree layer of the Acm5 unit (the “m” stands for temporary ponds, “mares” in French) is mainly composed of *Sclerocarya birrea* and *Balanites aegyptiaca* whereas the bushes are mainly *Guiera senegalensis* and *Boscia senegalensis*. Woody cover in small depressions of the plains is higher. Near temporary ponds, species like *Adansonia digitata*, *Acacia nilotica* (L.) Willd. ex Del., *Ziziphus mauritiana*, *Commiphora africana* and *Grewia bicolor* are found. The grass layer is dominated by *Schoenefeldia gracilis*, *Eragrostis tremula* (Lam.) Hochst. ex Steud., *Alysicarpus ovalifolius*, and *Zornia*

glochidiata. The grassland of the Ferlo have also been classified by Valenza and Diallo (1972b) in “formations” according to the soil type and relief, “groups” and “grassland types” according to the composition of the woody and herbaceous layer (See Appendix 6).

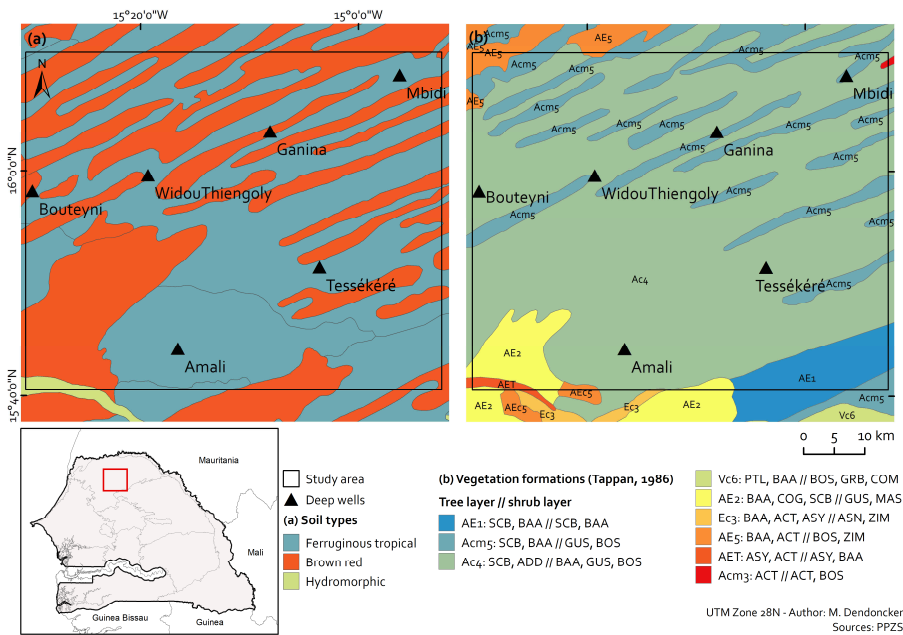


Figure 3.1 – Soil types (a) and vegetation types (b) inside the study area. Major species of the vegetation formations are displayed by a three letters abbreviation: ACT: *Acacia tortilis*, ADD: *Adansonia digitata*, ASN: *Acacia senegal*, ASY: *Acacia seyal*, BAA: *Balanites aegyptiaca*, BOS: *Boscia senegalensis*, COG: *Combretum glutinosum*, COM: *Commiphora africana*, GUS: *Guiera senegalensis*, GRB: *Grewia bicolor*, PTL: *Pterocarpus lucens*, ZIM: *Ziziphus mauritiana*.

3.2.2. Soils hydric properties

Direct measurements of soil properties and humidity are rare. To highlight the role of topography on soil water balance, we present here some work carried out in Fété-Olé, an area of the sandy pastoral region, 35 km northeast of Widou Thiengoly (Figure 2.4), similar to our study area in terms of soil types (ferruginous tropical soils). The rainfall regime in Fete-Olé is also similar to the one observed in Widou these last 35 years (see 3.2.3).

The distribution of roots along the profile is linked to the soil water content. Poupon (1980) dug up 49 trees (belonging to the species *Commiphora africana*, *Balanites aegyptiaca*, *Grewia bicolor*, *Boscia senegalensis*, *Acacia senegal* and *Guiera senegalensis*) to observe their root system. He saw that the taproots never reached beyond three meters depth while the lateral roots mainly spread in the 50 first centimeters.

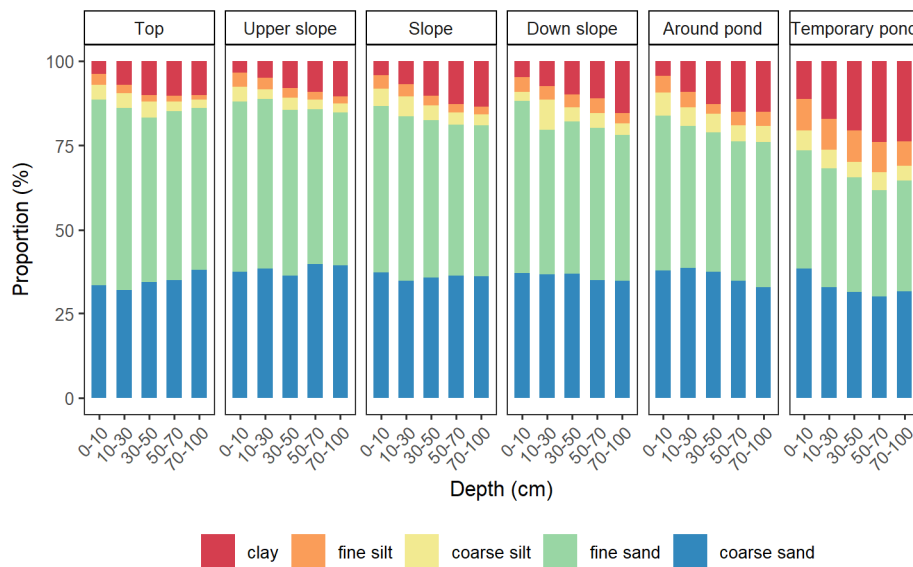


Figure 3.2 – Grain size repartition in the first meter along a toposequence in Fété-Olé.
Created with data from Cornet (1976).

Hydric properties of soils depend on the soil grain size, which slightly change according to the topography. Cornet (1976) studied the physical properties of the soils and the water balance in Fété-Olé. He measured the soil grain size of the first meter along a toposequence (from the top of a dune to a temporary pond, Figure 3.2) and its humidity from zero to three meters depth. We can see in Figure 3.2 that the sand ratio (fine sand and coarse sand) is high whatever the depth and whatever the topography. From the surface to deeper and from the top to downhill (around pond and in temporary pond), the clay content increases and is twice as high in depression as on top. Fine silt content is also higher downslope, around pond and in pond. Soil humidity at a given pF depends on the soil content in fine elements (clay and fine silt) and hence the topography. Cornet (1981) gives the values of soil humidity, at retention capacity, field

capacity (pF 2.5) and wilting point (pF 4.2), according to the depth and for a toposequence element (Appendix 7).

Cornet also studied the temporal evolution of the available water by measuring it during four years, from 1975 to 1978, according to the topography (Cornet, 1981; Figure 3.3). The topography, through run-off from tops to down slope, influences the water distribution. The water distribution between three soil layers (0-30 cm, 30-100 cm and 100-300 cm) can be consulted in Appendix 7. Beyond 300 cm, Cornet stated that the soil is nearly always dry as the re-wetting front rarely attains this depth.

The year 1975 was a normal year with 311.2 mm of rainfall. The rainfall of the years 1976 and 1978 was slightly in excess with 346.4 and 340.1 mm whereas 1977 was a dry year with only 126.2 mm. In 1975, on tops and slopes, the depth of infiltration reached 150 -180 cm in early September; deeper, the soil stays dry all year round. Water reserve is empty starting 1 October. Down slope, the water reached 100 cm in July and exceeded 300 cm in August. Some available water remained at the end of the dry season (i.e. in May 1976), a phenomenon that will not be observed again for the following years. In 1977, a dry year, we can see that available water is only present down slope but the profile is already dry at the very beginning of the dry season. In 1978, rainy episodes are more intense, which cause a low infiltration in top and slope and an increase run-off toward downslope.

These observations highlight the importance of considering topography when studying woody vegetation in this zone. Indeed, the different topographic positions present contrasted water balance, because of the difference in the soil composition and the run-off inflows. The available water is higher down slope because of the soil grain size and the water input from run-off.

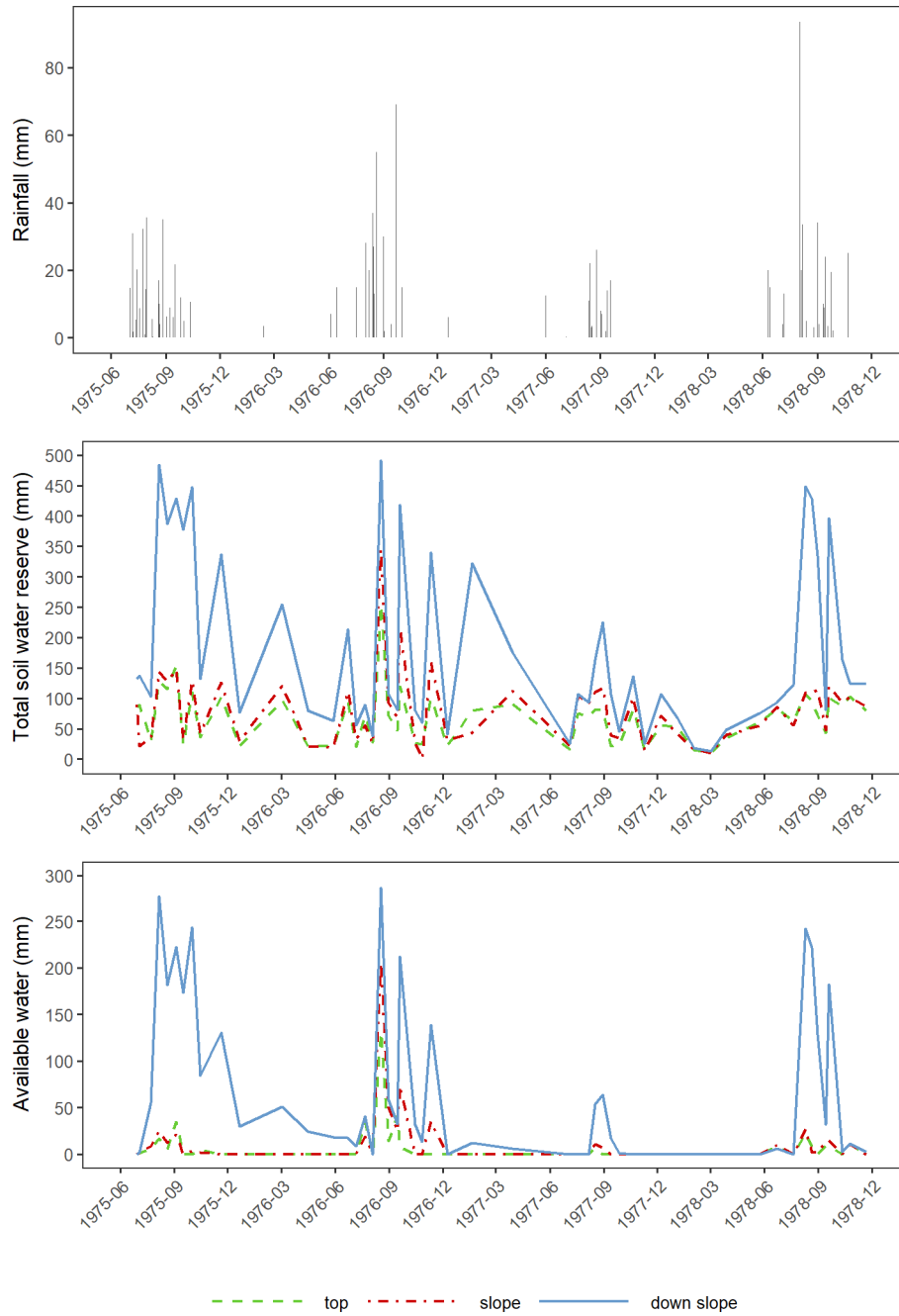


Figure 3.3 – Daily precipitations from 1975 to 1978, evolution of the water content and the available water reserve (total from zero to 300 cm depth) from 1975 to 1978 according to the topography. Created with data from Cornet (1981).

3.2.3. Climate data

3.2.3.1 Available data and selected indicators

Climate data are difficult to obtain for West Africa, either due to a lack of reliable gauging station or because of government policies. Besides, there are sometimes great variation between sources. For our study area, we used two different sources of climate data (Table 3.1). The first one concerns the exact location of Widou Thiengoly. Annual rainfall are available from 1940 to 1980 and starting from 1981, daily records took over. The second source was made available via the PPZS and comes from an internal database of Agrhymet – IRD. For three locations close to our study area (Dagana, Dahra and Linguère, Figure 2.4), daily records of rainfall are available from 1933 to 2002 and daily records of temperatures (minimal, maximal and mean) from 1950 to 2002.

Table 3.1 – Climate datasets features.

Source	Station	Coordinates		Type of data	Period
		Lat	Long		
Agrhymet database	Dagana	16.51° N	15.50° W	daily rainfall	1935-2002
	Dahra	15.35° N	15.48° W	daily rainfall	1935-2002
	Linguère	15.39° N	15.11° W	daily rainfall	1935-2002
				daily temperatures	1950-2002
Local measures	Widou	15.99° N	15.32° W	annual rainfall	1940-1980
				daily rainfall	1981-2015

From these datasets, several indicators were calculated. Indeed, using multiple indicators instead of the annual amount of rain helps to better apprehend the temporal distribution and the intensity of rainy events. As an illustration, Lebel and Ali (2009) studied the recent trends in rainfall in the Central and Western Sahel using several indicators. They found that the periods 1970-1979, 1990-2007 presented an annual rainfall deficit compared to the period 1950-1969, and that this deficit was caused by a decrease in the number of rainy days rather than a decrease in the rainy events intensity. As the temporal distribution of the rains is important for the vegetation (e.g. woody vegetation could profit from early and late rains, contrary to herbaceous layer; Brandt *et al.*, 2019), it is important to consider other indicators than the total amount of rainfall to characterize the rainfall regime.

The annual rainfall equals the sum of daily rainfall. The annual means of rainfall, maximal and minimal temperatures were calculated. The annual number of rainy

days is the number of days with an amount of fallen water superior to 1 mm. The Standardized Precipitation Index (SPI; McKee *et al.*, 1993) compares the cumulated rainfall on a given temporal scale with a reference chronology for one site. This allows the characterization of a drought event in a standardized way, each event being linked to a probability of occurrence (Table 3.2). Three other indices (Simple Daily Intensity Index, mean gap between two rainy days and Sahelian annual rainfall index) are presented in Appendix 8.

Table 3.2 – Classification of precipitation regime according to SPI values.

Range of SPI values	Precipitation regime	Probability of event (%)
>2.0	Extremely wet	2.3
[1.5, 2.0]	Very wet	4.4
[1.0, 1.5]	Moderately wet	9.2
[-1, 1]	Normal precipitation	68.2
[-1.5, -1]	Moderately dry	9.2
[-2, -1.5]	Very dry	4.4
-2.0	Extremely dry	2.3

The length of the rainy season, in days, was also calculated. Usually, in the study area we consider that the rainy season starts in July and ends in October. However, if we want to consider the effective vegetation growth period, we need to take account of the actual onset of rains. Several definitions of the beginning of the rainy season exist as mentioned in Sivakumar *et al.* (1993). In their study, they used the following criteria to determine the beginning and the end of the rainy season to compute the length of vegetation period in Niger. The date of the onset of the rains (X) is when, after May 1, the quantity of precipitations during three consecutive days reaches at least 20 mm and when no drought period of more than seven days is recorded during the 30 following days. The end of the rainy season (Y) is after September 1, when there is no rain at all for 20 consecutive days. The length of the vegetation period, in number of days, is then computed by $Y - X$. However, the quantity of rain falling in our study area is so low that the condition of “no drought period of more than seven days is recorded during the 30 following days” is never achieved. So we chose to apply the definition of the Famine and Early Warning System (FEWS) used in Salack *et al.* (2011). The onset of rains is defined as the first day of a decade that cumulates a rain amount of 25 mm and that is followed by two decades that have a rain amount of at least 20 mm. The end of the rainy season follows the same criteria as Sivakumar *et al.* (1993).

3.2.3.2 Indicators: annual rainfall and temperatures

The mean annual rainfall of the four stations (Table 3.3) illustrates the north-south rainfall gradient, with Dagana, the most northern station having the lowest mean rainfall (262.6 mm) and Dahra and Linguère, both at the same latitude having the highest rainfall. As expected, the minimum rainfall was observed during the great drought, in 1983, except for Dahra. Annual rainfall can be classified according to the quintiles of the distribution from high deficit to high excess (Cornet, 1978; Figure 3.4). In Widou, between 1972 and 1984, i.e. during the great drought, 10 years are classified as in deficit or in high deficit.

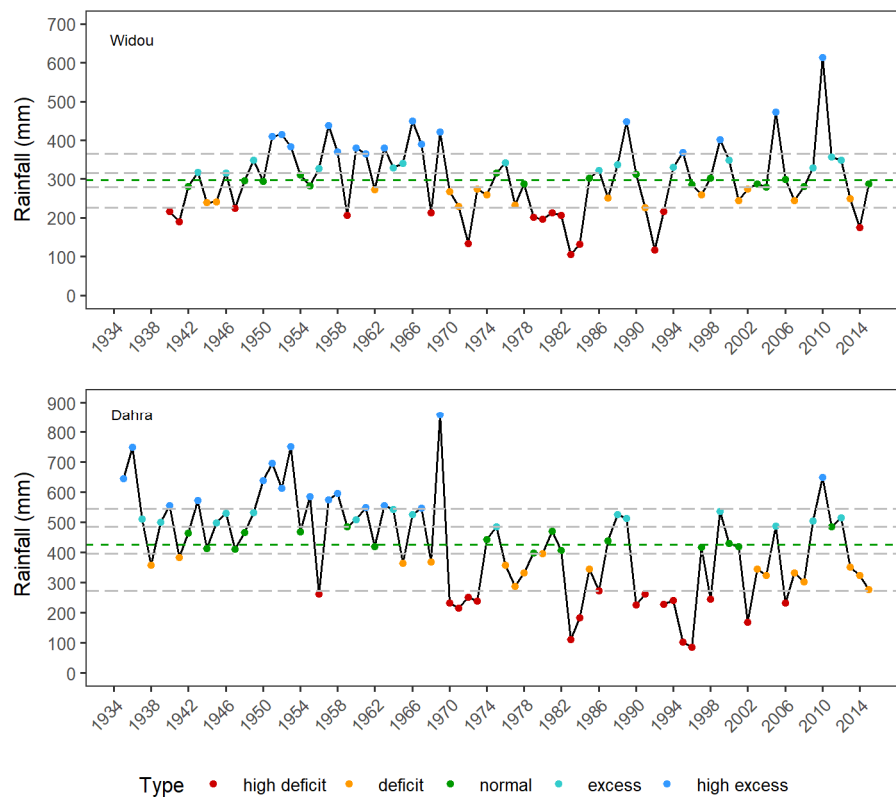


Figure 3.4 – Annual rainfall in Widou Thiengoly and Dahra (see Figure 2.4 for location), classification according to Cornet (1978). Grey dashed lines represent the quintiles of the distribution and green dashed lines are the averages.

Table 3.3 – Annual rainfall (mm) statistics: mean and standard deviation, maximum and minimum with the year during which the max-min was observed between brackets.

Station	Mean ($\pm$ sd)	Max	Min
Dagana (1935-2002)	262.6 $\pm$ 87.8	492.3 (1955)	46.9 (1983)
Dahra (1935-2002)	430.2 $\pm$ 161.5	858.0 (1969)	85.4 (1996)
Linguère (1935-2002)	446.6 $\pm$ 135.2	853.6 (1936)	189.9 (1983)
Widou Thiengoly (1940-2015)	297.6 $\pm$ 87.5	613.8 (2010)	105.4 (1983)

The annual temperatures (mean, min and max) for Linguère are illustrated in Figure 3.5. The mean and minimum annual temperatures are generally increasing since the beginning of the observations in 1950. The maximal temperatures are more constant and stay between 34 and 38°C. According to the IPCC, the estimated changes in temperatures from 1986-2005 to 2081-2100 in West African Sahel are comprised between +1 to +1.5°C according to the RCP 2.6 scenario (i.e. the “best” case) and +4 to +5°C according to the RCP 8.5 scenario (i.e. the “worst” case). In both scenarios, more than 90% of the models agreed on the predicted changes (IPCC, 2014b). The trends for rainfall are less certain. RCP 2.6 scenario predicts between -10% and +10% of rainfall amount and RCP 8.5 scenario gives the figures of -10% to -20% (IPCC, 2014b).

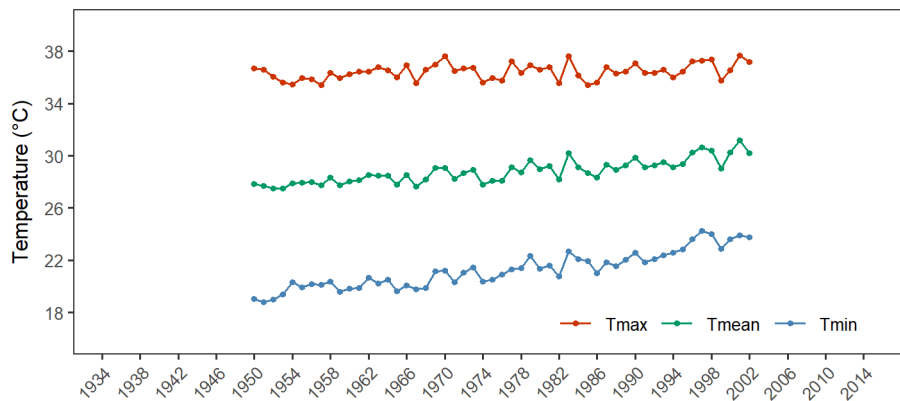


Figure 3.5 – Annual temperatures in Linguère (see Figure 2.4 for location) from 1950 to 2002.

Two indicators characterizing precipitation are represented in Figure 3.6 for Dahra and Widou. First, the number of rainy days has decreased in Dahra since 1933. This trend is not visible in Widou as the series starts in 1981. The length

of the rainy season is highly variable, ranging from 170 days to zero in 1983 for Dahra and in 1992 for Widou.

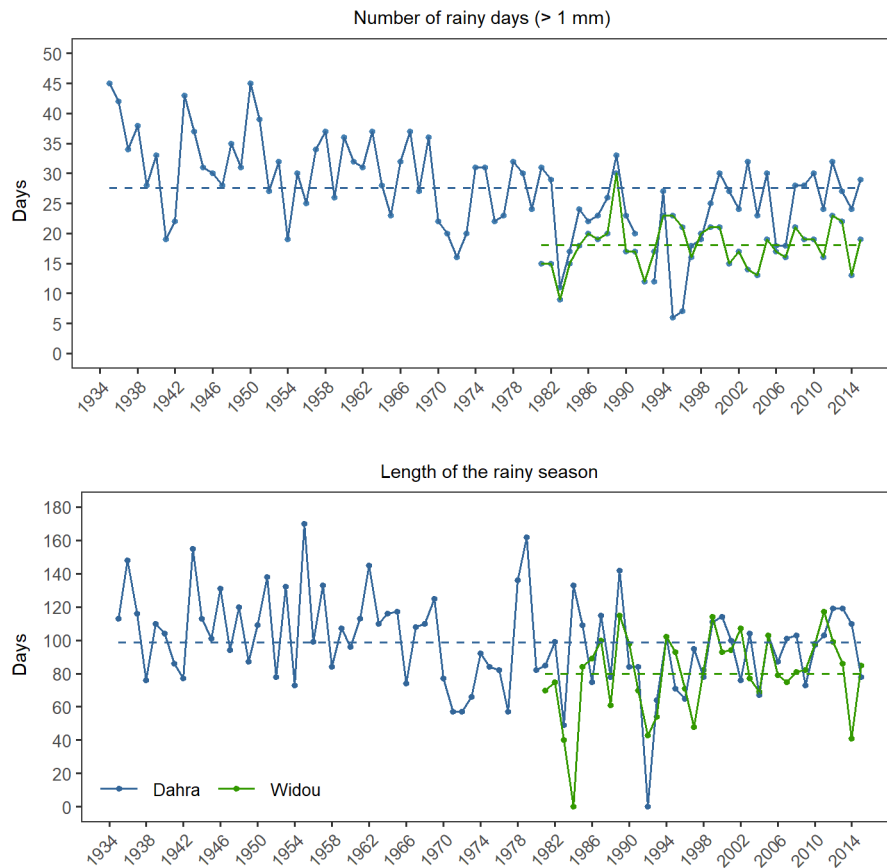


Figure 3.6 – Number of rainy days and length of the rainy season in Dahra (1935-2015) and Widou (1981-2015). The dotted lines represent the means.

The identification of the “driest” year really depends on the indicator (see Table A8.1 in Appendix 8). For Widou, the year 1983 appears to be the driest when it comes to water amount, with a total rainfall of 105.5 mm and nine days of rain. However, in 1984, there has been no rainy season (according to the definition used in this work) and this year presents the lowest Simple Daily Intensity Index with 8.8 mm per rainy episode. The SPI (Figure 3.7) shows that if we analyze the rainfall over the entire series (since 1934), the driest years are, as expected, 1983-1984, during the great drought. However, the years 1992, 1995 and 1996 are also

characterized by a SPI value less than -2. Table A8.1 in Appendix 8 gathers the indicators for the stations of Linguère, Dagana and Dahra. Even though the stations are located at less than 130 km from each other, the indicators are quite different, which illustrates the high spatial variability of Sahelian rainfall.

The analyses conducted on the rainfall data show that even though the most severe drought occurs in the 1970s-1980s at the Sahelian scale, what we consider as the driest years depend on the location and on the indicators. Besides, the SPI also identified some years outside the great drought period that are as dry as during the drought.

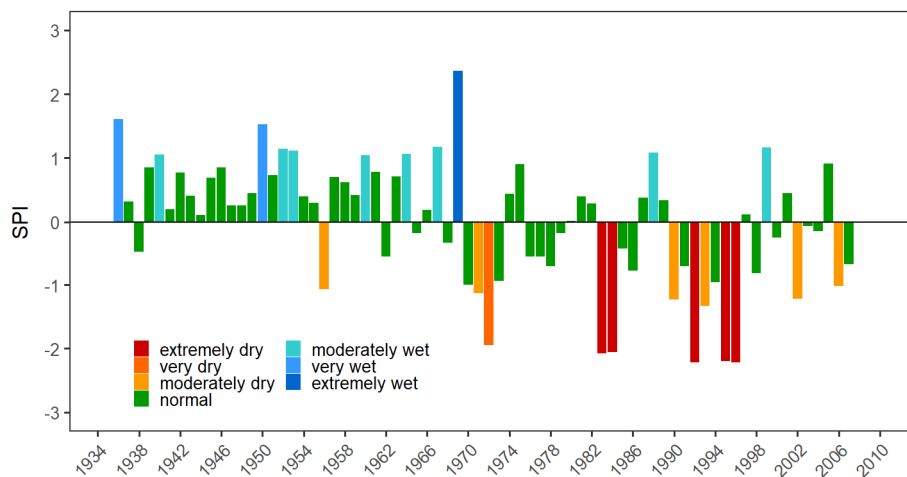


Figure 3.7 – SPI in Dahra for September, calculated on a 3 months width window.

As stated in Chapter 1, the study of long-term dynamics is organized in three periods, based on the West African Sahel rainfall series. The first period is before the great drought (1960-1971), for which the total rainfall of 8 years is classified as “in excess” within our study area (Figure 3.4). SPI values in Dahra mostly belong to the “normal” or “moderately-very-extremely wet” categories (Figure 3.7). The last two years of this period mark the early stages of drought with the total rainfall of 1970 and 1971 in deficit. The second period is the great drought (1972-1984). The year 1972 is chosen as the beginning of the period as it is the driest year recorded at the Sahelian scale since 1913 (Bille, 1974; Poupon and Bille, 1974) and 1984 as the last very dry year, before the wetter years 1985-1988 (Nicholson, 2001; e.g. Figure 3.4). The period 1972-1984 presents 10 years of total rainfall in “deficit” or “high deficit” in Widou (Figure 3.4). We also observe

a decrease in the number of rainy days (Figure 3.6) and an increase of the minimum temperatures (Figure 3.5). The third period, after the great drought, is characterized by a slight increase of the number of rainy days (compared to the previous period, Figure 3.6), though with 3 years marked as “extremely dry” by the SPI in Dahra (Figure 3.7). Total rainfall seems to slightly recover with 21 years classified as “normal”, or “excess” in Widou, from 1985 to 2015 (Figure 3.4).

3.2.4. Populations and livestock

Pastoral families are organized in camps (or settlements), each of them being “a residential unit of a family group, organized into one or multiple houses (*gallé* in Fulani)” (Manoli *et al.*, 2014). A settlement can be the home of the families of two brothers, each of them responsible for their respective *gallé*. If the house chief has several wives, his *gallé* will be composed of several households (Barral, 1982; Manoli *et al.*, 2014). Some daily life decisions are taken at the settlement level and others at the *gallé* level (Manoli *et al.*, 2014).

The Fulani settlements are numerous inside the study area. However, few recordings from field studies are available. As the presence of a camp could influence the vegetation in the surroundings (through wood collection or grazing by livestock), we located the position of the settlements. Fulani settlements are well visible from the sky: houses and fences build for the flocks have recognizable geometric forms and the ground in the immediate surroundings appears darker, due to the accumulation of organic matter from animal’s feces.

We used three datasets in order to record the settlements at three dates: (i) the satellite imagery of Bing map from 2013 (© Bing Map Microsoft); (ii) the WorldView-1 VHR images from April 2008 (© 2015 Digital globe, Inc. Licensed under Nextview); (iii) the aerial photographs taken in January or February 1980. On each of these data sets, we are able to distinguish the camps as illustrated in Figure 3.8.

The Bing map images and the WorldView-1 cover all our study area, whereas the aerial photographs are only available for the Tessékéré zone (see section 3.3.3). The camps have been recorded inside the study area (58 km x 65 km; Figure 3.8) by applying a cell grid of 2 km x 2 km. In each cell, camps have been marked by hand. We can see on the map that the camps are gathered and aligned in longitudinal bands that are in fact the plains, as seen in section 3.2.1 (see Figure 3.1). For the recording of 2013, we were able to detect the number of *gallés*. We

gathered the gallés in a single settlement if those were located at less than 250 m from each other. We then created a typology for the camps in 2013 according to their number of gallés. We recorded 953 camps, composed of 1 to 11 gallés, which represents a density of 0.27 camps.km⁻². Inside the two 15 km radius circles around the deep wells of Widou and Tessékéré, the density is a little higher with 0.32 camps.km⁻². The analysis of aerial images from 1980 around Tessékéré shows a much lower density with 0.10 camps.km⁻² (see Appendix 9).

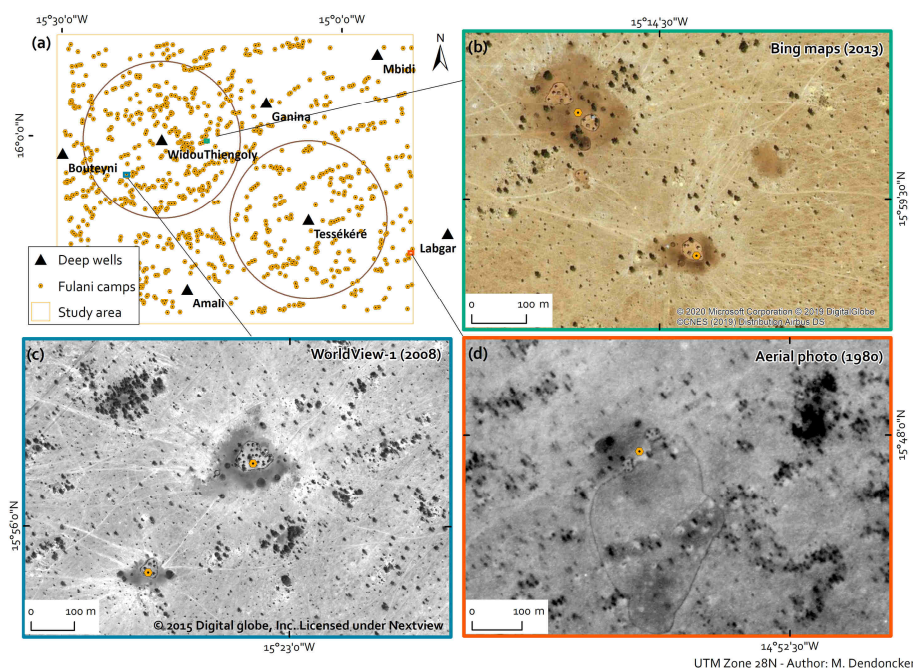


Figure 3.8 – Camps location inside the study area (a) and examples of camps views from: Bing map aerial (2013, b); WordView-1 (2008, c, © 2015 Digital globe, Inc., Licensed under Nextview); aerial photos (1980, d).

The number of camps gives an estimation of the anthropic pressure that is exerted inside our study area. We can have an estimation of the number of persons based on the number of gallés. Barral (1982) conducted surveys in the north-west Ferlo (including Widou and Tessékéré deep wells) and mentioned that the average number of persons that occupy one gallé is around 10. Therefore, we estimated the population to 16 087 within the study area and to 7 128 inside the service area (two circles of 15 km radius) of the two studied deep wells (Appendix 9, Table A9.1). These numbers are equivalent to a density of 4.5

to 5 inhabitants.km⁻². Assouma (2016) estimated the population within the service area of Widou (15 km radius) in 2015 to 4 676 persons, which represents a density of 7 inhabitants.km⁻². As a comparison, the population density for Senegal is estimated at 71 persons.km⁻² in 2014, with the most populated regions located on shores (Cesaro *et al.*, 2010; May *et al.*, 2015; Figure 2.3). Other Sahelian countries with large desert areas, such as Mali and Chad, present lower densities with 13 and 10 persons.km⁻² respectively (May *et al.*, 2015).

The fact that herders hardly communicate about the size of their herds and the pastoral mobility are factors that contribute to make the assessment of livestock units difficult and uncertain (Cesaro *et al.*, 2010). We gather here the few data that exist in the literature for the area around Widou Thiengoly. The first assessment that we found dates back to 1989. Using CSE (Centre de Suivi Ecologique) data, Mieke *et al.* (2010) cite a number of 9 520 head of cattle and 18 552 sheep and goats. The ECLIS project made an estimation of 12 330 head of cattle and 34 550 sheep and goats in 2010 (Touré *et al.*, 2011). The latest reference gives the numbers of 16 108 head of cattle, 43 131 sheep and 20 532 goats within the service area of Widou Thiengoly (Assouma, 2016).

3.3. Description of the datasets

3.3.1. Field inventory dataset

Fieldwork was organized in two phases. The first one was conducted in April, August and September 2015. The purpose of these inventories was to get a fully detailed picture of the current state of woody vegetation inside the study area. A stratified sampling was applied according to the topography and the distance to the studied deep wells. We inventoried 139 plots of 0.25 ha each around the deep wells of Widou Thiengoly and Tessékéré (Figure 3.9). This plot surface corresponds to the minimal area recommended for studying woody vegetation in the Sahel (Boudet, 1984).

The plots were arranged on ten axes, at seven distances: 2, 3.5, 5, 7.5, 10, 12.5 and 15 km from the deep wells (20 plots per distance). For each distance, we randomly selected at least six plots in depressions (43 plots in total), the other plots being located on slopes or on hilltops (96 plots in total). Whenever possible, the plots in each category of topography were distributed between the two soil types. In total, 86 plots were allocated to the ferruginous soils and 53 plots to the

sub-arid brown red soils. The list of the inventoried plots, their coordinates, topography and soil type is in Appendix 10.

In every plot, all the trees, bushes and shrubs were counted separating them into living, dead and regeneration, i.e. the individuals with a circumference below 10 cm. Among the regeneration, two classes were distinguished: (i) the seedlings, i.e. individuals with a height below 30 cm and (ii) the saplings, i.e. individuals with a height above 30 cm. For each living individual, we recorded the species and we measured its circumference at 30 cm from ground level and its crown diameter in two perpendicular directions. The height was determined with an ultrasound device for trees with a height greater than 3 m and visually estimated for smaller shrubs.

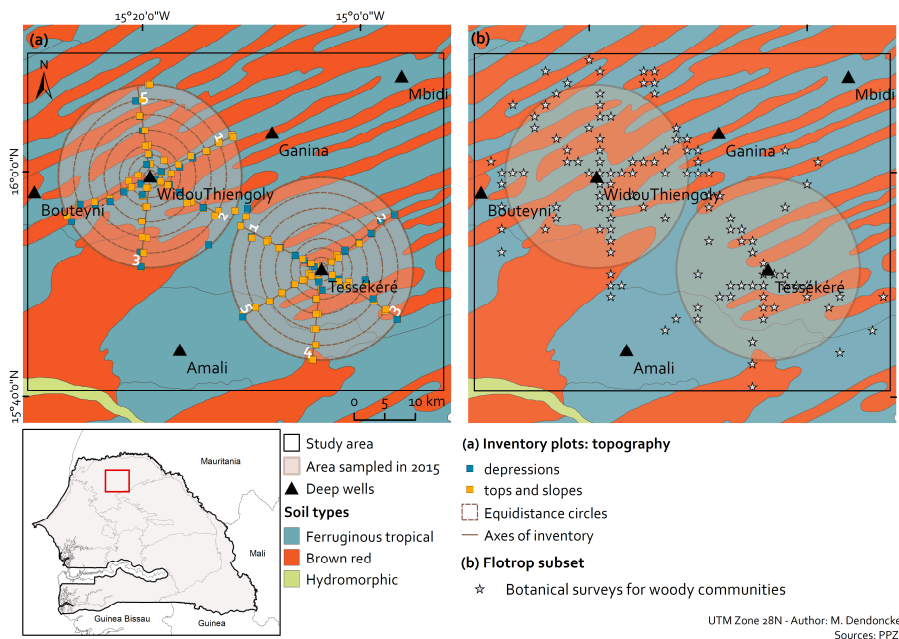


Figure 3.9 – Field surveys within the study area. (a) Plots inventoried in 2015. White numbers serve as identifiers of the axes. (b) Historical botanical surveys from the Flotrop database subset used in this study. Several observations are superposed, making the number of stars smaller than the actual number of observations (278 records).

The second phase was carried out in December 2017. This fieldwork was designed to validate the WorldView-1 analyses (see section 3.3.3 for the description of this dataset and Chapter 5 for related analyses). Thirty plots were

inventoried in the area around Tessékéré. The plots were allocated equally between dunes and plains in a way to represent a wide range of woody cover. These plots are part of the study sites for the temporal dynamics (Chapter 5; see Appendix 10 for the list and coordinates). We recorded every individuals with a GPS point. The species was recorded and the crown diameter was measured in two perpendicular directions. The percentage of overlapping crowns between the trees was visually estimated.

3.3.2. Flotrop: an historical vegetation database

Flotrop is a vegetation database that gathers numerous plant observations conducted in northern tropical Africa, between 1920 and 2012 by several contributors (Daget and Gaston, 1999; Taugourdeau *et al.*, 2019). The observations target both herbaceous and woody communities. The exact methodology (e.g. the size of the inventoried surface) that was applied for the botanical surveys are unknown. However, observations can be classified in several types, including phytosociological unweighted surveys, which correspond to a list of species recorded in one station and phytosociological weighted surveys, which express species abundances with Braun-Blanquet coefficients (Braun-Blanquet, 1932). Though all the observations in the database are geotagged, the locations have often been determined after the study, based on topographical map and notes from the author. The consequence is that the precision of the locations is around 1 minute, which approximately corresponds to 1.8 km in this area (thus preventing us of attributing a local topographic element per record).

A subset of this database corresponding to an area of 20 km radius around the deep wells of Widou Thiengoly and Tessékéré was used in this study (Figure 3.9). The collection dates of the 278 selected records range from 1965 (one record) to 1997 (one record), the majority of the surveys were carried out between 1970 and 1986 (Figure 3.10). Among them, 143 records belong to the category of “phytosociological weighted surveys”. The Braun-Blanquet coefficients were transformed into relative abundances by dividing each abundance by the sum of the individual abundances. The other 135 records contain information about the presence of species, i.e. “unweighted phytosociological surveys”.

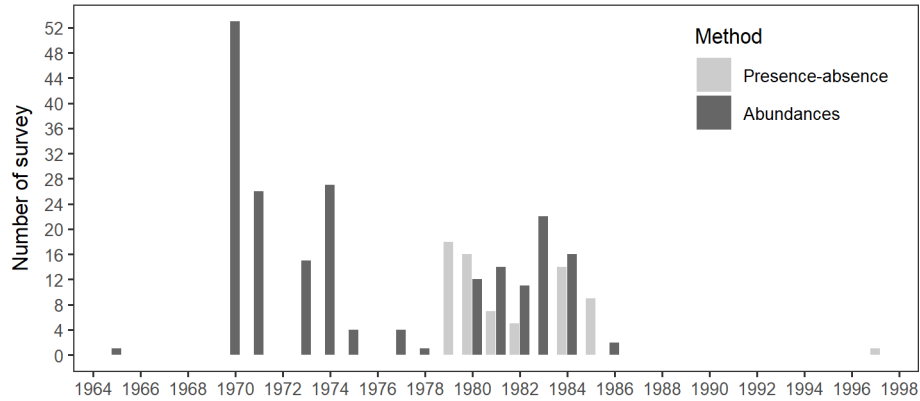


Figure 3.10 – Temporal repartition of the Flotrop records according to the method.

3.3.3. Geographical and remote sensing dataset

In the frame of this work, a large amount of geographical data has been gathered from different institutions (mainly the PPZS and the CSE) but also from literature and paper maps that have been scanned, georeferenced and converted into shapefiles (vector data) manually. These data served as basis to elaborate the different protocols. As some data are rare and were not easy to acquire, we decided to list them in this section, hoping they can be helpful for future studies. A more complete list of GIS data is presented in Appendix 11.

Three maps appeared to us as the most important. The first one maps the morphopedology by Tappan (1986). The second is a map of the vegetation units as defined in Tappan, (1986, see Figure 3.1 for a preview of these two maps). The third one is a map of another vegetation classification (Valenza and Diallo, 1972b; see Appendix 6, Figures A6.1 and A6.2). These maps were georeferenced, using cities or deep wells as ground control points before being digitalized into polygons.

In addition to these GIS data, we used four EO datasets (Table 3.4). The first dataset are Corona images of 1965 available from the U.S. Geological Survey. These images needed to be georeferenced prior to use. Using Bing map as base map, Corona images were first roughly positioned using the coordinates referenced by the USGS for each image. Then, ground control points were fixed, using recognizable large trees or deep wells.

Table 3.4 – Characterization of the Earth observation datasets.

Dataset	Date	Number of images	Approximate area covered by one image	Resolution (m)
Corona	1965	5	1000 km ² (16 km x 70 km)	2 to 4
Aerial photo	1980	31	120 km ² (11 km x 11 km)	0.6
Worldview-1	2008	12	300 km ² (17 km x 17 km)	0.5
Bing aerial	2018	unknown	unknown	unknown

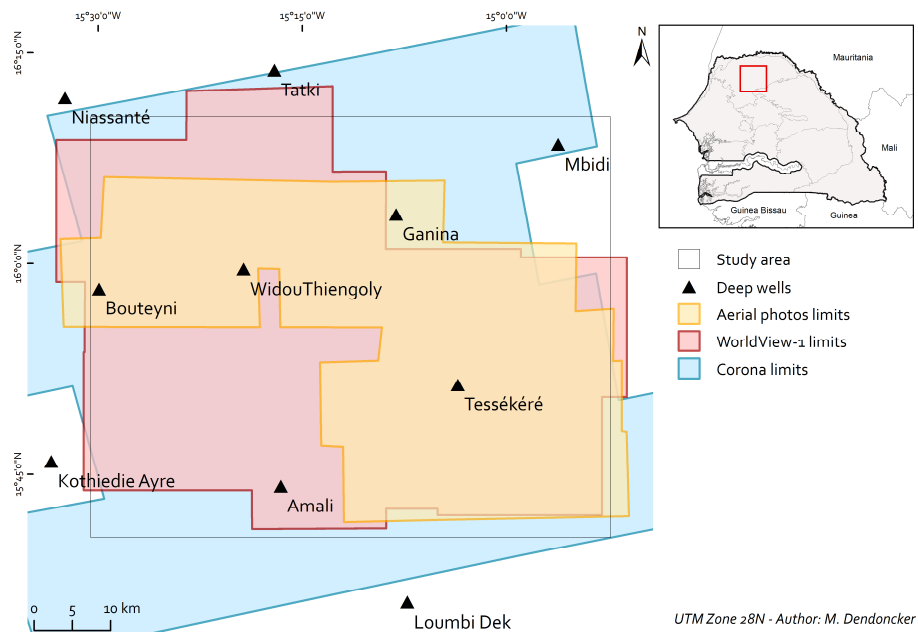


Figure 3.11 – Earth observation datasets coverage.

The second dataset are the aerial photographs taken in January or February 1980, by the Teledyne society for the OMVS at a scale of 1:50 000 (Guissé *et al.*, 1987). The University of Copenhagen provided some of these photos. The rest of them were bought from the Agence Nationale de l'Aménagement du Territoire in Dakar. Unfortunately, the photos were among thousands of photos presenting with no filing system so we did not manage to find the entire series of photos that would have covered all of the study area. Besides, the quality of this second batch is lower due to the poor scan quality (the negatives were not available and it was not allowed to borrow the original images on paper to scan them elsewhere).

The third dataset contains WorldView-1 VHR images from April 2008 that were provided by NASA as part of a collaboration agreement (© 2015 DigitalGlobe, Inc. Licensed under NextView). The last dataset is the satellite imagery of Bing map from 2013 (© Bing Map Microsoft). The spatial coverage of these four datasets are represented in Figure 3.11.

3.3.4. Species functional traits dataset

The trait-based approach (Chapter 6) required the collection of traits values for a list of species. The species concerned were the ones inventoried during the fieldwork and the ones recorded in the phytosociological weighted surveys of the Flotrop database (section 3.3.2). In total, traits values were gathered for 39 species (list in Appendix 12).

The list of traits for which information were collected was established in several steps. A first list was set up by taking account of the traits easily measurable (e.g. the plant height), or largely used in the literature (e.g. SLA). The list was then completed by searching for plant features related to the response to drought, fire or grazing and/or having an effect on two ecosystem functions: biogeochemical cycles and primary productivity. The paper of Cornelissen *et al.* (2003) was taken as reference to establish a first list which was further completed by a wider literature review. For each pressure and function, we searched the literature for the association of the pressure and function name with the terms “traits” or “functional diversity”. In some cases, though not systematically, the mechanisms behind the link between traits and disturbances were explicitly enounced in some references. This search was completed according to our knowledge of the processes.

For some of the traits that were found to be linked to the disturbances and functions, data were largely missing for our species list. They were therefore discarded from the trait-based approach. The traits were gathered in “response sets” and “effect sets”. Appendix 13 gathers the complete list of traits per pressure and function, including the ones that were not used in this work; the list of sources that linked traits to response and effect; and the mechanisms if mentioned in the literature.

We present hereafter, and in Table 3.5, the traits that were used in this research, classified in different groups according to what part of the plant they describe or what function they express. We retained the five classes of Pérez-Harguindeguy *et al.* (2013): whole plant traits, leaf traits, stem traits, belowground traits and

regenerative traits. Citations inside quote come from Pérez-Harguindeguy *et al.* (2013). Not all the features collected are actual “traits” according to the definition of Violle *et al.* (2007) some are features used as proxy for hard traits (section 2.4.1).

Whole plant traits:

- Growth form (form): as explained in section 2.2.3, we distinguish three types of growth form in the frame of this work: tree, bush and shrub;
- Maximum height (h.max): “plant height, or maximum height, is the maximum stature a typical mature individual of a species attains in a given habitat”, so it represents the optimum height at a given site;
- Spinescence: “refers to the degree to which a plant is defended by spines, thorns and/or prickles”.

Leaf traits:

- Digestible proteins (pr.dig): fraction of the proteins in the foliage that are actually digested by livestock, expressed in proportion of dry matter;
- Leaf area (lf.ave): the surface of one side of a leaf;
- Leaf area category (lf.siz): classification of the area of a leaf in three groups. While it is less precise (because categorical) than leaf area (continuous), it has the advantages to be more reliable because simpler and easier to find in the literature;
- Leaf phenology or duration of leafing period (lf.mth): number of months during which the plant bears leaves. Proxy for “leaf lifespan” which is straightforward for deciduous species but more difficult to establish for evergreen species that may change their leaves every year or keep the same leaves during several years;
- Leaf persistence (lf.per): indicates if the plant bears leaves all year round (evergreen) or not (deciduous);
- Leaf N and P content (lf.N, lf.P): content of nitrogen/phosphorus contained in leaves per unit of dry mass;
- Specific leaf area (SLA): “one-sided area of a fresh leaf, divided by its oven-dry mass”.

Stem traits:

- Bark thickness (bk.th): normally, this trait corresponds to the thickness (in mm) of the part of the stem that is external to the wood or xylem. However, as this information was not available for our species, we classified the barks in three categories, from 1 (thin bark) to 3 (thick), according to our field knowledge and flora;

- Specific stem density (wd.den): for woody species, that corresponds to the wood density. It is a proxy for the xylem resistance to embolism (Santiago et al., 2016);
- Vessel area (vs.are): the surface of the vessel lumen in the transversal direction. This trait is used as a proxy for xylem resistance to embolism (Sankaran, 2019).

Belowground traits:

- Nitrogen fixer (N.fix): categorical trait (yes or no) expressing the ability of a plant to fix nitrogen from the atmosphere;
- Presence of a taproot (tprt): trait used as a proxy for the root length, for which no information was available.

Regenerative traits:

- Dispersal mode or dispersal syndrome (disp): indicates the way that the seed, fruit or spore (the unit in charge of the dissemination of the plant) is being disseminated. It indirectly informs about the distance the seed might travel;
- Fruit length (fr.lg): size of the largest dimension of the fruit;
- Resprouting capacity (cop): “capacity of a plant species to resprout after destruction of most of its above-ground biomass”;
- Root suckering capacity or clonality (rt.suc): “the ability of a plant species to reproduce or regenerate itself vegetatively”.
- Seed weight (sd.w): “the oven-dry mass of an average seed of a species, expressed in mg”.

The traits values of the 39 species were gathered in a large matrix in which we noted the source for each record. The sources that were used are varied: flora, the TRY database (Kattge *et al.*, 2011), journal articles (see Appendix 14 for the list of the references consulted). As the TRY database gathers a considerable amount of traits values (Kattge *et al.*, 2011), we started by entering several requests in order to obtain the maximum amount of information about the species. The list of traits requested in TRY is in Appendix 14. For some traits, we completed the matrix according to our field knowledge (e.g. Burke, 2006; Schmidt *et al.*, 2013; Walker *et al.*, 1999).

Table 3.5 – List of the traits used in this study, per category. The last column indicates in percent for how many species the trait values were found. Traits are listed alphabetically within each category.

Traits	Type	Units or attributes	Completeness (%)
Whole-plant traits			
Growth form (form)	categorical	tree, bush, shrub	100
Maximum height (h.max)	continuous	m	100
Spinescence (spin)	ordinal	from 1 (no spine) to 4 (numerous, hard, long spines)	100
Leaf traits			
Digestible protein (pr.dig)	continuous	% of dry matter	74
Leaf area (lf.ave)	continuous	mm ²	59
Leaf area category (lf.siz)	categorical	nanophyllous (20-200 mm ²), microphyllous (2-6 cm ²), submicrophyllous (6-20 cm ²), mesophyllous (20-100 cm ²).	72
Leaf N content (lf.N)	continuous	mg.g ⁻¹	90
Leaf P content (lf.P)	continuous	mg.g ⁻¹	82
Leaf persistence (lf.per)	categorical	deciduous, evergreen, semi-evergreen	100
Leaf phenology (duration of leafing period) (lf.mth)	continuous	months	87
Specific leaf area (SLA)	continuous	mm ² .mg ⁻¹	41
Stem traits			
Bark thickness (bk.th)	ordinal	from 1 (thin) to 3 (thick)	100
Stem specific density (wood density) (wd.den)	continuous	g.cm ⁻³	92
Vessel area (vs.ave)	continuous	mm ²	59
Below-ground traits			
N fixer (N.fix)	categorical	yes or no	87
Presence of a taproot (taprt)	categorical	yes or no	46
Regenerative traits			
Dispersal mode (disp)	categorical	anemochorous, zoochorous	97
Fruit length (fr.lg)	continuous	mm	90
Resprouting capacity (coppice) (cop)	categorical	yes or no	87
Root suckering capacity (rt.suc)	categorical	yes or no	72
Seed weight (sd.w)	continuous	mg	97

This matrix was then simplified to be readable in R software. To do so, some rules and guidelines have been followed to deal with the cases where different values were available for one trait. We took the mean of the different sources for

the continuous traits (e.g. wood density). If the trait was categorical, we chose the value according to the reliability of the source or we took the mean of occurrences (e.g. if a species is mentioned three times as being dispersed by zoochory and one time by anemochory, the ‘zoochorous’ attribute is retained). We also paid attention to the location of the trait measurement (in case of doubt between two values, we took the study the nearest from our study area). Finally, in some cases where no data existed we used the mean for the genus (e.g. wood density).

3.4. Summary: datasets, methods and chapters

In this chapter, we presented the datasets that are used in this work (field inventory data, vegetation database, remote sensing data and literature data). Some of them are integrated in more than one chapter, as shown in Figure 3.12. Field inventory data of 2015 are mobilized in all the chapters. Field data of 2017 are integrated at the temporal dynamics (in Chapter 5). The Flotrop database is part of Chapter 5 and Chapter 6 (about functional diversity). The remote sensing data are mobilized in Chapter 5. Literature data about species functional traits are the foundation of Chapter 6.

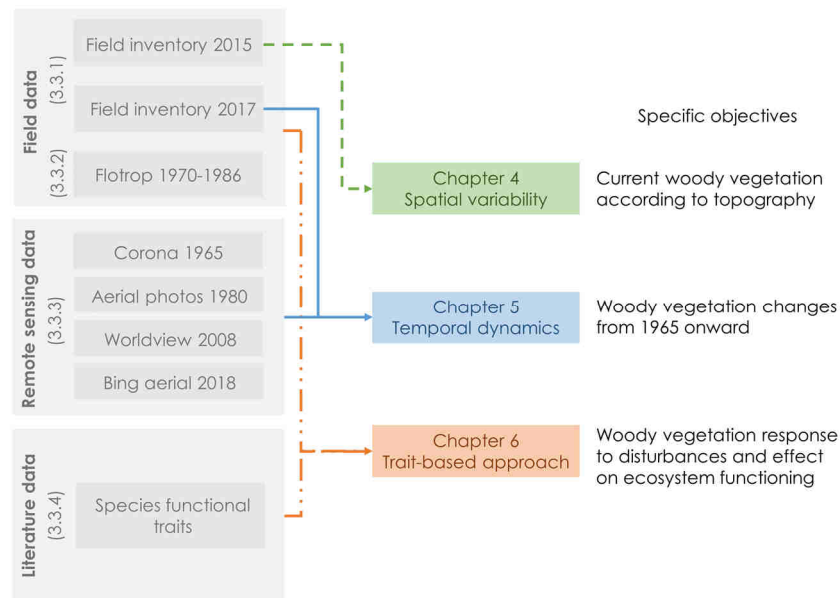


Figure 3.12 – Summary of the datasets used and their integration in the different chapters of the thesis.

Chapter 4

Spatial variability of current woody vegetation and its regeneration

— *Outline* —

In this chapter, current woody vegetation is studied according to the topographic position and the remoteness of deep wells. These two factors are proxies for water availability and anthropogenic activities. Specific composition, density, woody cover, regeneration and population structure are analyzed on 139 inventory plots. The text of this chapter comprises the paper of Dendoncker M. and Vincke C. (2020) *Low topographic positions enhance woody vegetation stability in the Ferlo (Senegalese Sahel)*, Journal of Arid Environments, 175, 104087. This chapter can therefore be read as a “standalone” chapter, which involves some repetitions regarding the state of the art (Chapter 2) and methodology (Chapter 3). In addition to the paper, the results of two complementary analyses have been added. The first one is the Importance Value Index (IVI), which highlights the ecological importance of species by taking into account their density, their cover and their frequency. The second is the study of the specific composition of saplings communities via Principal Coordinates Analysis.

– *Abstract from JAE* –

Woody vegetation provides multiple services to the pastoralists in the Sahel and since the drought of 1972–1984, concerns have been raised about its persistence. Some studies have observed a decline in tree density and specific richness while others have reported a greening at a larger scale. In this study, an extensive field inventory was carried out around two deep wells in the Ferlo (Senegal). The influence of topography and proximity of deep wells on woody vegetation density, diversity and regeneration was studied. An analysis of the size class distribution was carried out to gain insight into the population dynamics of some species. This study highlights the key role of low topographic positions in favoring woody vegetation establishment with a higher species richness and a greater density. The remoteness of deep wells seems to have no effect on these variables. The instability of several tree species populations was evident from the size class analysis. As large trees play an important role in hosting regeneration, the persistence of the current woody vegetation is threatened. Given the positive impact of depressions on woody vegetation, further research should focus on these topographic features and their role as central pieces in a potential management plan.

4.1. Introduction

Sahelian ecosystems face many challenges given the water scarcity in the region (mean annual rainfall from 200 to 600 mm), the high climatic variability, and the long-standing and increasing anthropic pressures. Indeed, the rains are not only concentrated during a short three-month wet season, but they also have a high spatial and inter-annual variability (Nicholson, 1995). In addition, the population of Sahelian countries, which reached 135 million in 2014, keeps increasing with annual growth rates of 2.5 to 4% (May *et al.*, 2015).

Savanna with annual grasses constitutes the typical Sahelian vegetation. It can be further characterized according to the height of woody species as shrubby or wooded savanna, and according to the density of trees, as open or scattered savanna (Hiernaux and Le Houérou, 2006). The most limiting factor for woody vegetation development in the northern Sahel is water availability; the variability of woody communities is mostly impacted by the water regime, which depends on the annual rainfall, the soil type and the local topography (Cornet, 1992; Hiernaux and Le Houérou, 2006).

During the 1970s-1980s, the Sahel experienced the most extreme drought of the 20th century. Dry conditions persisted during the 1990s with a mean August rainfall from 1968 to 1997 35% lower than the mean rainfall between 1931-1960 (Nicholson, 2013). Since this extreme climatic event, which was then followed by a general increase of mean temperatures (Brandt *et al.*, 2014), considerable research has focused on herbaceous and woody communities and have highlighted a trend of decreasing species richness and woody cover (Epule *et al.*, 2014). For instance, Gonzalez *et al.* (2012) found a reduction in tree density and species richness from 1960 to 2000 on three sites in the Western Sahel. Hänke *et al.* (2016) also observed a shift in woody vegetation composition toward drought tolerant species in Burkina Faso. Others have found an increase in population density and woody cover in sandy soils, but a continuing decrease in the shallow soils of eroded surfaces in Gourma (Mali, Hiernaux *et al.*, 2009).

On the other hand, some studies have observed a general increase in the NDVI on a large scale across the Sahel since 1980 (Dardel *et al.*, 2014; Herrmann *et al.*, 2005). However, this greening needs to be characterized at the local scale to correctly interpret this phenomenon. For instance, Herrmann and Tappan (2013), while reporting an increase in NDVI and leaf biomass at several greening sites in the central Senegal, has indicated through field inventory, a decline in species richness along with an increase in bush cover to the detriment of mature

trees. Brandt *et al.* (2015) observed the same trend in the Ferlo region in Senegal. From a long term perspective, scientists don't know yet if this greening is an indication of a return to conditions prior to the 1970s -1980s drought, or is rather a shift to another equilibrium state with a different vegetation composition (Herrmann *et al.*, 2005).

These discrepancies highlight the necessity to characterize the woody vegetation structure and fitness in the Sahel at the species population scale. This need is that much more important when we consider the multiple species-specific ecosystem services provided by the woody vegetation (Bremen and Kessler, 1995; Le Houérou, 1980c). The Ferlo, a sylvo-pastoral area in the Senegalese Sahel, with typical Sahelian ecosystems and bio-climate, illustrates this interdependence between climate, woody vegetation and land use. The Fulani people, the major ethnic group of Ferlo, mainly rely on raising livestock for a living. For this population, woody vegetation is a very valuable resource as it provides fuel and construction material in addition to fodder for livestock, especially at the end of the dry season, when the grass layer is completely depleted. Assouma (2016) reported that in 2014-2015 the contribution of tree browsing to the cattle's diet was found to be of 48% from March to June and 14% over the whole year.

Since the 1950s, multiple deep wells were installed in the Ferlo, leading to major changes at social and environmental levels. Indeed, these deep wells allowed permanent access to the Maastrichtian aquifer, in an area that was previously unoccupied during the dry season because of the lack of fodder and water (Thébaud and Batterbury, 2001). Consequently, modifications in the pattern of seasonal transhumance were observed along with some changes in the vegetation with deep wells becoming permanent attractors of human settlements (Thébaud, 1990). In the northern Ferlo, Vincke *et al.* (2010) showed increasing trends, although not statistically significant, of the species richness, and the density and regeneration of woody vegetation with increasing distance from the deep wells. In addition to these permanent settlements in the immediate vicinity, many small human settlements are scattered in the study area. These camps are composed of a few houses and small enclosures for the livestock.

Given these current trends and the ecosystem services provided by trees and shrubs, it is relevant to question the persistence of woody vegetation in this zone. More specifically, it is crucial to gain knowledge about the actual state of woody vegetation (which species are present and where, what woody cover is present and characteristics of their population and regeneration) in order to be able to discuss its stability amidst current and future disturbances. To precisely capture

the spatial variability of woody vegetation characteristics, we completed a field inventory in order to determine the influence of two environmental filters on the woody vegetation: water availability and anthropogenic pressure.

Water availability varies according to the local topography position (depressions vs hilltops and slopes) of several meters drop, which also goes along with changes in soil texture and organic matter content. In this study, we use local topography as a proxy for water availability. The anthropogenic pressure considered here includes all the woody and non-woody products collection linked to human settlement in the immediate vicinity of deep wells, which would influence the species density. As the deep wells facilities attract people and animals, we expect that the farther we move away, the less pressure there is on woody vegetation up to a maximal distance value where we enter the influence zone of another deep well.

This research has two specific objectives. The first is to study the effects of topography and distance to deep wells on the spatial distribution, the specific composition, the density and the woody cover of ligneous communities. We hypothesize that (i) the positions of low topography (i.e. depressions) would promote tree establishment and fitness; and that (ii) the farther we move away from deep wells, the higher will be the density and species richness. The second objective is to gain insights into woody vegetation dynamics by analyzing the regeneration and the population structures of several species, i.e. the distribution between adults and regeneration, using a Size Class Distribution approach. We hypothesize that these structures are influenced by the two environmental filters, and that low topographic positions would host more balanced populations with higher regeneration rate.

4.2. Material and methods

4.2.1. Study area

The study area is located in the northern part of the sandy Ferlo (Senegal) and is part of the “sylvo-pastoral reserve of the six deep wells”. The reserve status means that land use is restricted to pastoral activities with no agriculture aside from subsistence farming. We studied the vegetation inside two areas with a 15 km radius⁷, centered on two deep wells present since 1956 (Barral, 1982):

⁷ These two areas are a subset of the study area of the present thesis, as we considered a rectangle of 68 km x 55 km centered on these two deep wells for the rest of the work.

Widou Thiengoly (15.99° N, 15.32° W) and Tessékéré (15.85° N, 15.06° W, Figure 4.1). These deep wells were chosen for two reasons: (i) their representativeness of the sandy Ferlo deep wells in terms of population and flow rate; and (ii) the availability of historical data such as meteorological measurements and previous inventories. Between 1940 and 2015, the study area received a mean annual rainfall of 297.6 ($\pm$ 87.5) mm with a minimum of 105 mm during the drought in 1983.

The major relief of Ferlo is formed by an alternation of fossil aeolian sand dunes oriented southwest – northeast, measuring 10 to 30 m high and 0.5 to 5 km wide. The dunes are separated by longitudinal plains of 1 to 5 km wide (Le Houérou, 1989). This landform contains the two major soil types encountered in the area: the ferruginous tropical soils and the sub-arid brown red soils (Figure 4.1). The ferruginous tropical soils on the dunes are slightly acidic sandy soils. They contain less than 1% of organic matter and their upper horizon is leached of iron and clay (Le Houérou, 1989). The brown subarid soils are located at the bottom of the large plains in which the temporal ponds are formed during the rainy season (Le Houérou, 1989). The ratio of sand reaches 90% but the clay and organic matter contents are slightly higher than in the ferruginous tropical soils (Le Houérou, 1989). The local topography superposes itself to these two macro relief elements. Many small depressions of several meters in depth are found on the plains as well as on dunes though to a lesser extent and with different soil properties (Stancioff *et al.*, 1986).

According to Stancioff *et al.* (1986), who mapped the vegetation resources of Senegal, two major vegetation units are found inside our study area⁸. The first unit is dominated by three tree species, *Sclerocarya birrea* (A. Rich.) Hochst., *Balanites aegyptiaca* (L.) Del., and *Combretum glutinosum* Perr. ex DC., and it is encountered on sandy to clayey soils of aeolian origin. The second unit, on the plains, is mainly composed of *Balanites aegyptiaca*, *Acacia seyal* Del., *Adansonia digitata* L., *Acacia nilotica* (L.) Willd. Ex Del. and *Sclerocarya birrea*.

The number of livestock, and therefore the grazing pressure, has increased since 1950 inside the study area. Cattle numbers increased tenfold from the beginning of the 20th century to 1982, and sheep and goat numbers have increased even more (Diop *et al.*, 2003). Using the CSE (Centre de Suivi Ecologique) data from 1989, the number of cattle has been estimated at 9 520 head and sheep and goats at 18 552 within a radius of 15 km around Widou (Miehe *et al.*, 2010). In the same

⁸ See Figure 3.1 in this document.

area, Assouma (2016) assessed the number of cattle at 16 108 head and sheep and goats at 63 663 head during the year 2014.

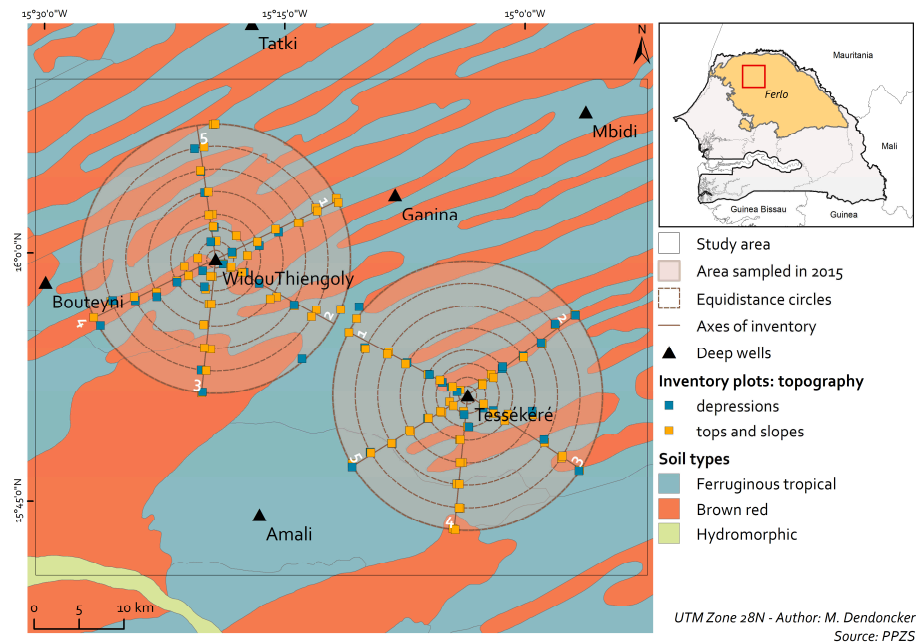


Figure 4.1 – Location of the inventoried plots and soil types in the study area. The white numbers identify the axes of inventory per deep well. The detailed regeneration analysis was carried out on axes 2 to 5 around Tessékéré and on axe 4 around Widou.

4.2.2. Sampling and inventory measurements

A stratified sampling was applied according to the topography and the distance to the studied deep wells. In 2015, we inventoried 139 plots of 0.25 ha each around the deep wells of Widou Thiengoly and Tessékéré (Figure 4.1). This plot surface corresponds to the minimal area recommended for studying woody vegetation in the Sahel (Boudet, 1984). The plots were arranged on ten axes, at seven distances: 2, 3.5, 5, 7.5, 10, 12.5 and 15 km (20 plots per distance). For each distance, we randomly selected at least six plots in depressions (43 plots in total), the other plots being located on slopes or on hilltops (96 plots in total). As the distinction between hilltops and slopes is not always straightforward in the field, we combined these two topographic elements into one single class for the analyses. The size of the depressions containing the plots varies between 0.12 ha to 3 ha, based on visual estimation in the field, and cross-checked with Bing map

satellite imagery. We focused our inventory beyond the first two kilometers from the deep wells. Closer than two kilometers, the area is clearly impacted by houses, vegetable gardens and drinking troughs, as observed in the field and on the Bing aerial satellite imagery. The soil therefore suffers heavy trampling from herds, preventing the growth of vegetation. Whenever possible, the plots in each category of topography were distributed between the two soil types. In total, 86 plots were allocated to the ferruginous soils and 53 plots to the subarid brown red soils.

We also paid attention to three factors that could potentially influence woody vegetation. Firstly, the plots were located at a distance of at least 500 m from any Fulani camp in order to minimize the most likely influence of these numerous camps on the immediate surrounding vegetation. This distance was chosen according to field knowledge. The position of the camps was determined from the analysis of the Bing map images from April 2013 (Appendix C⁹). Secondly, the Widou Thiengoly area has been part of two projects. The first project is a grazing trial that was set up in the 1980s by a Senegalo-German cooperation (Miehe *et al.*, 2010) and during which some experimental plots were fenced to prevent the passage of livestock. The second project is the still ongoing Panafrican project of the Great Green Wall, where some reforestation plots have been established. We have been careful not to locate our inventory plots inside these experimental perimeters. Thirdly, even if the impact of bush fires is far less important than in the Sudanian zone, fires can still destroy woody regeneration (Bremen and Kessler, 1995). As the MODIS products indicate that there were no fires inside our study area from November 2013 to September 2015, we assume that this disturbance has had a minimal influence on our analysis.

The total surface occupied by the local depressions represents about 6% of the study area (i.e. the two 15 km radius circles). This estimation was made after the field work and is based on the woody cover map at a resolution of 2 m draw by Brandt *et al.* (2018) from which we derived a map of local topography. We first aggregated the woody cover map at a resolution of 50 m. We then determined for each pixel if it should be classified as hilltop or depression based on a woody cover threshold. This threshold corresponds to the lower limit of a 99% confidence interval applied on the woody cover distribution calculated after the map of Brandt *et al.* (2018) for the inventoried plots located in depressions.

In every plot, all the trees, bushes and shrubs were counted separating them into living, dead and regeneration, i.e. the individuals with a circumference below

⁹ Appendix 9 in this document.

10 cm. Among the regeneration, two classes were distinguished: (i) the seedlings, i.e. individuals with a height below 30 cm and (ii) the saplings, i.e. individuals with a height above 30 cm. For each living individual, we recorded the species and we measured its circumference at 30 cm from ground level and its crown diameter in two perpendicular directions. The height was determined with an ultrasound device for trees with a height greater than 3 m and visually estimated for smaller bushes. For the multi-stemmed shrub species (i.e. *Boscia senegalensis* (Pers.) Lam. ex Poir. and *Calotropis procera* (Ait.) Ait. f.), the perimeter was taken for the group of stems, as a whole, at ground level. As this measure overestimated the actual basal area given the gap between the stems, it was corrected by an empirical factor of 0.5. Species like *Grewia bicolor* Juss., *Guiera senegalensis* J. F. Gmel., *Feretia apodanthera* Del. and *Bauhinia rufescens* Lam. can sometimes present themselves as multi-stemmed bushes. However, all of the individuals encountered during our inventory were bushes with one to three trunks, so we applied the same measurement method as for trees. Regarding the woody cover values, computed from the crown diameter, it should be noted that the any overlap among canopies (a typical case is the presence of several *Boscia senegalensis* under a large tree) has not been measured. This means that the woody cover, calculated as the sum of the individual crown cover, overestimates the actual part of the ground that is covered by the projection of tree crowns.

For the regeneration of all species, with the exception of *Boscia senegalensis*, *Calotropis procera* and *Leptadenia pyrotechnica* (Forssk.) Decne.¹⁰, a detailed analysis was conducted on 70 plots (47 located on hilltops and 23 in depressions), on axes 2 to 5 around Tessékéré and on axe 4 around Widou (Figure 4.1). The reason for this subset is the combination between the lack of workforce on the field and the maintenance of the representativeness of the two topographic elements and soil types. The analysis was carried out during August 2015, which is ideal timing to study regeneration as the first rains would have made the seeds sprout, and grasses would not yet be tall enough to hide the seedlings.

On this subset of plots, we noted if the regeneration was established under the shade of the canopy. We did so for each sapling and seedling or for each group of regeneration, a group being defined as a gathering of five or more individuals, in an area of one square meter. We also measured (i) the distance between the regeneration and the nearest adult tree, shrub or bush of any species, and (ii) the distance between the regeneration and the nearest adult *of the same species*, if we found one in a radius of a hundred meters around the regeneration. For each

¹⁰ The regeneration of these three species was very abundant.

nearest adult, we recorded the following features: species, height, crown diameter and circumference. For all the regeneration analyses and unless stated otherwise, we used the data of this subset (August 2015) to avoid an underestimation of the number of seedlings. Indeed, the first fieldwork took place in April when seeds have not yet sprouted, and the last fieldwork was carried out in September, during the mature phase of the herbaceous vegetation cycle when the tall grasses hide the seedlings. In the following analyses and discussion, after the initial reference to a species, we will subsequently refer to the species with the genus name when there is only one species for this genus in order to simplify the reading of the results and discussion.

4.2.3. Data analyses

4.2.3.1 Influence of the environmental factors

We conducted a thorough description of the tree stand for each topographic element (i.e. hilltops vs depressions). The woody cover ($\text{m}^2.\text{ha}^{-1}$), the basal area ($\text{m}^2.\text{ha}^{-1}$), the density of the adults, saplings and seedlings were calculated for each plot and each species. Based on the proportion of depressions inside the study area (i.e. the two 15 km radius circles), calculated after the woody cover map (section 4.2.2), we also computed the weighted means for the overall 139 plots.

To allow the study of the impact of environmental factors on the species composition in one single analysis, we chose to represent the species distribution of the 139 plots in a multidimensional space with a Principal Coordinates Analysis (PCoA). A Bray-Curtis dissimilarity matrix was calculated from the matrix of species abundances at the adult phase. The influence of multiple environmental factors (topography, soil type, and distance to the nearest deep well) on the first two axes of the PCoA were tested using ANOVA or linear regression (for distance to the nearest deep well). The deep well distance is the distance between each plot and the nearest deep well taken among all that are present in the area (not only Widou and Tessékéré), assuming that all of them are equivalent in terms of attractiveness. All the analyses were performed in R software (R core team, 2018).

The influence of topography was tested with Welch t-test on the following response variables: the specific richness of adults and saplings; the densities for adults, saplings and seedlings; the basal area ($\text{m}^2.\text{ha}^{-1}$); and the woody cover ($\text{m}^2.\text{ha}^{-1}$). The same analysis was conducted to verify if the soil type had an influence on the parameters listed above. Normality of the data was graphically

checked by computing a normal qq-plot and numerically by calculating the Skewness and Kurtosis coefficients. If these indicators were close to the values taken by normal data set (i.e. three for Kurtosis and zero for Skewness), the data were analyzed in their original form. In the other cases, a mathematical transformation (square root or logarithm) was applied to normalize them. The generated p-values were adjusted using Holm's procedure in order to minimize errors due to multiple testing. While the sampling design was not planned to compare the two topographic elements according to their belonging to the relief category (dunes and plains), we tested this effect a posteriori by comparing the means of richness, density, basal area, and woody cover.

The influence of distance from deep wells was tested on the same variables as those considered in the topography analysis. In addition, the proportion per distance of the eight most abundant species were also studied (i.e. *Acacia tortilis* subsp. *raddiana* (Savi) Brenan, *Acacia seyal*, *Balanites aegyptiaca*, *Boscia senegalensis*, *Calotropis procera*, *Guiera*, *Grewia*, *Sclerocarya*). We applied three types of models according to the type of the response variable (discrete or continuous), using the R stats package. The first one is the linear regression (*lm* function), applied to data that were close enough to normal data in their original form or after a transformation by logarithm or square root (i.e. the woody cover and the densities). The second type is the Generalized Linear Model (*glm* function) with a quasi-Poisson law as the link function (to account for the over-dispersion) which was applied for the specific richness, a discrete and counting variable. The third type is a nonlinear model (exponential decay) with least square adjustment (*nls* function), which assumes the normality of the variable and was used for species ratio. In all the models, the tested factor is the distance in kilometers between each plot and the nearest deep well among those present in the area including Ganina and others (Figure 4.1). The plots were divided according to the topography for all analyses on deep well remoteness.

4.2.3.2 Population structure and size class distribution analysis

The population structures were described via an analysis of the Size Class Distribution (SCD). This type of analysis is a way to obtain information about the population dynamics from static data of the vegetation structure at one given time (Sop *et al.*, 2011). These structures are indeed the result of the recruitment, growth and mortality processes that have been acting for many years on the woody plant population (Wiegand *et al.*, 2000). The analysis of size class has been used in other research studying the viability of woody species population in arid

zones along with their regeneration abilities and their long-term dynamics (Lykke, 1998; Sop *et al.*, 2011; Wiegand *et al.*, 2000).

We studied the species for which more than 15 individuals were recorded. This threshold, set arbitrarily in order to avoid having too few individuals by class, is superior to the one used by Hänke *et al.* (2016) in their study of the vegetation dynamics in northern Burkina Faso (10 individuals). The analysis was therefore applied to *Acacia tortilis*, *Balanites aegyptiaca* and *Sclerocarya birrea* for both topographic elements; to *Acacia seyal*, *Grewia bicolor* and *Guiera senegalensis* for the depressions; and to *Acacia senegal* (L.) Willd. for the tops. *Boscia senegalensis* and *Calotropis procera* were excluded from our analysis because of their wide distribution and their growth form. Indeed, the relationship between circumference and stage of maturity does not have the same meaning for the multi-stemmed shrubs as for the trees.

The size class analysis can be decomposed in four steps. Firstly, the individuals were gathered into circumference classes of 10 cm. The ones with a circumference above 200 cm were assigned to the 190-200 cm class to avoid having too few individuals in the last classes. A linear regression was applied between the midpoint of the classes as the independent variable and the number of trees in each class as the dependent variable. We used a log transformation ($\log + 1$) of both variables to obtain straight lines (Sop *et al.*, 2011). The slope of the regression is an indicator of the population regeneration capacity (Condit *et al.*, 1998; Lykke, 1998). A high negative slope will express a good regeneration rate, as more individuals will be in the first classes, whereas a slight negative or a positive slope will indicate a small regeneration rate or a void recruitment.

Secondly, the quotients between the numbers of individuals in successive classes were computed. The mean of these quotients and particularly its standard deviation, evaluate the population stability¹¹. Stable quotients, identified by small standard deviations are the sign of a stable population (Sop *et al.*, 2011).

Thirdly, we calculated the permutation index (PI, Wiegand *et al.*, 2000), which compares the actual curve of the population structure with a monotonous slope that would be expected in the case of an undisturbed population structure for which a negative exponential curve would be observed (Sop *et al.*, 2011). The permutation index is equal to the sum, for every class, between the difference of its expected rank and its actual rank in terms of number of individuals (Sop *et al.*,

¹¹ Note: this notion of population stability is not equivalent to the stability concept developed in Chapter 2.

2011). For example, in an ideal population, the class of 0 to 10 cm should have the greatest number of individuals and hence the first rank. The higher the PI is, the more the studied population will have a discontinuous class distribution (Wiegand *et al.*, 2000).

$$PI = \sum_{i=1}^n |J_i - i| \quad (1)$$

Where J_i is the rank of class i and vary between 1 and n , the number of size classes; and i is the actual rank.

Finally, the Simpson's index of dominance was computed. This index is a measure of the occupation equality between classes (Wiegand *et al.*, 2000). The values of this index stretch from zero to one. A negative exponential distribution of an ideal population would have an index of 0.1. For a more detailed interpretation of PI and C, see Wiegand *et al.* (2000).

$$C = \frac{\sum_i N_i \times (N_i - 1)}{N \times (N - 1)} \quad (2)$$

N is the total number of trees and N_i is the number of tree in the class i .

4.2.3.3 Regeneration features

Based on the subset of 70 plots, the ratios between the number of seedlings and the total number of adults and seedlings were computed for each species and for each topographic element. We did the same for the saplings. These ratios (i.e. the seedlings rate and the saplings rates) are called hereafter the regeneration rates. The immediate surroundings of the regeneration were characterized by (i) gathering the mean features of the nearest adult (circumference, height, crown diameter) and (ii) computing the average distance between the regeneration and the nearest adult for each species of the regeneration. These distances were then compared with a Kruskal-Wallis test followed by a pairwise Wilcoxon test (with p-values adjustment using Holm's method) to check for interspecific differences.

To evaluate if the establishment of species was influenced by woody cover, we assigned to each seedling and sapling the feature “under canopy” or “outside canopy” according to the position of the regeneration below or outside the crown of adults. Akpo and Grouzis (1996) pointed out that woody cover enables the regeneration by offering suitable conditions for germination and growth, and

by attracting the livestock to the shade, which drop seeds via their feces. To distinguish the *species* effect of woody cover, the ability of a particular species to host seedlings under its canopy was assessed by counting the number of seedlings for which the given species was the closest adult. This figure was then divided by the number of inventoried adults from the species. This “hosting index” represents the average number of seedlings that is being sheltered by an adult. The mean nearest distances between the regeneration and the adults were compared to the mean radius of the crown in order to verify if the “host effect” was related to the crown cover.

In 2015, the rainfall reached 287 mm, with a duration of the rainy season above the average and a mean gap between two rainy episodes of 5.5 days. The amount of rainfall put the year 2015 among the “normal” years according to the classification of Cornet (1978), the classification of the four previous years (from 2011 to 2014) being “excess”, “excess”, “deficit”, “strong deficit”. Therefore, our study has to be seen as a snapshot of the regenerative potential of woody vegetation for a year during which the rainfall is average.

4.3. Results

4.3.1. Influences of environmental factors on structure, composition and regeneration

On the 139 plots, 24 species belonging to 15 families were inventoried in the adult phase (Table 4.1, see Appendix A¹² for their counts and mean features). We also noted the presence of the liana *Leptadenia hastata* (Pers.) Decne; however, we did not included it in our analyses because of its growth form. The woody stand presents a mean crown cover of 6.5%, a basal area of 2.1 m².ha⁻¹ and a density of 42.5 adults per hectare. The densities of the saplings and dead woody plants are respectively of 37.1 ind.ha⁻¹ and 5.4 ind.ha⁻¹.

Among the 24 species that were inventoried at the adult stage, 13 species were found within both topographic elements. The species *Faidherbia albida* (Del.) Chev. was only encountered on hilltops and the 10 following species are only present in depressions: *Acacia ataxacantha* DC., *Acacia nilotica*, *Adenium obesum* (Forssk.) Roem. et Schult., *Anogeissus leiocarpa* (DC.) Guill. et Perr., *Bauhinia*,

¹² Appendix 15 in this document.

Combretum aculeatum Vent., *Dalbergia melanoxylon* Guill. et Perr., *Feretia*, *Stereospermum kunthianum* Cham. and *Ziziphus mauritiana* Lam.

Table 4.1 – Cumulated crown covers, adult densities and frequencies for all species encountered in depressions (D) and on tops (T). The species are gathered in three density groups. From top to bottom: species with more than 10 ind.ha⁻¹ (on at least one topographic element), species with 1 to 10 ind.ha⁻¹, species with less than 1 ind.ha⁻¹.

Inside each group, species are classified by alphabetical order.

Species	Abbr ev.	Crown cover (%)		Density (ind.ha ⁻¹)		Frequency (%)	
		D	T	D	T	D	T
<i>Balanites aegyptiaca</i>	BAA	10.4	1.5	47.6	6.9	79.1	53.1
<i>Boscia senegalensis</i>	BOS	2.0	0.6	66.6	18.4	81.4	67.7
<i>Calotropis procera</i>	CAP	0.7	<0.1	22.7	3.1	44.2	21.9
<i>Acacia seyal</i>	ASY	1.8	<0.1	3.9	0.0	25.6	1.0
<i>Acacia tortilis</i>	ACT	2.3	0.5	2.8	1.6	37.2	20.8
<i>Guiera senegalensis</i>	GUS	0.4	<0.1	1.7	0.3	16.3	2.1
<i>Grewia bicolor</i>	GRB	1.0	<0.1	4.2	0.2	46.5	5.2
<i>Sclerocarya birrea</i>	SCB	3.6	1.8	3.5	2.7	46.5	40.6
<i>Acacia ataxacantha</i>	ACA	<0.1	0.0	0.1	0.0	2.3	0.0
<i>Acacia nilotica</i>	ACN	0.7	0.0	0.4	0.0	7.0	0.0
<i>Acacia senegal</i>	ASN	0.4	0.2	0.7	0.6	11.6	7.3
<i>Adansonia digitata</i>	ADD	<0.1	0.2	0.2	0.2	4.7	4.2
<i>Adenium obesum</i>	ADO	<0.1	0.0	0.1	0.0	2.3	0.0
<i>Anogeissus leiocarpa</i>	ANL	0.4	0.0	0.2	0.0	4.7	0.0
<i>Bauhinia rufescens</i>	BAR	<0.1	0.0	0.1	0.0	2.3	0.0
<i>Combretum aculeatum</i>	COA	<0.1	0.0	0.1	0.0	2.3	0.0
<i>Combretum glutinosum</i>	COG	0.4	0.2	0.7	0.5	11.6	12.5
<i>Commiphora africana</i>	COM	<0.1	<0.1	0.1	0.0	2.3	1.0
<i>Dalbergia melanoxylon</i>	DAM	<0.1	0.0	0.1	0.0	2.3	0.0
<i>Faidherbia albida</i>	FAA	0.0	<0.1	0.0	0.0	0.0	1.0
<i>Feretia apodanthera</i>	FEA	<0.1	0.0	0.4	0.0	9.3	0.0
<i>Leptadenia pyrotechnica</i>	LEP	<0.1	<0.1	0.2	0.3	4.7	5.2
<i>Stereospermum kunthianum</i>	STK	0.2	0.0	0.2	0.0	2.3	0.0
<i>Ziziphus mauritiana</i>	ZIM	0.6	0.0	0.9	0.0	14.0	0.0
Total		25.0	5.3	157.5	34.9	-	-

The Principal Coordinates Analysis (Figure 4.2) highlights the influence of the topography on the second axis. The top side of the graph gathers mostly the plots located on tops, whereas the plots located in depressions occupy the bottom side. This effect is verified by an ANOVA ($P < 0.001$; $R^2=0.43$). The same trends were observed in the PCoA performed with the saplings abundances

(results not shown)¹³. The species usually found inside the depressions are on the bottom side, as *Anogeissus*, *Ziziphus* or *Acacia seyal* whereas species mostly present on hilltops (*Acacia tortilis*, *Adansonia digitata*) take the overhead positions. The second axis also reflects the soil type and the relief ($P < 0.01$) though with very low R^2 values of less than 5%, implying a weaker ecological effect. No influence of deep wells remoteness was found using linear regression for either axes ($P > 0.05$).

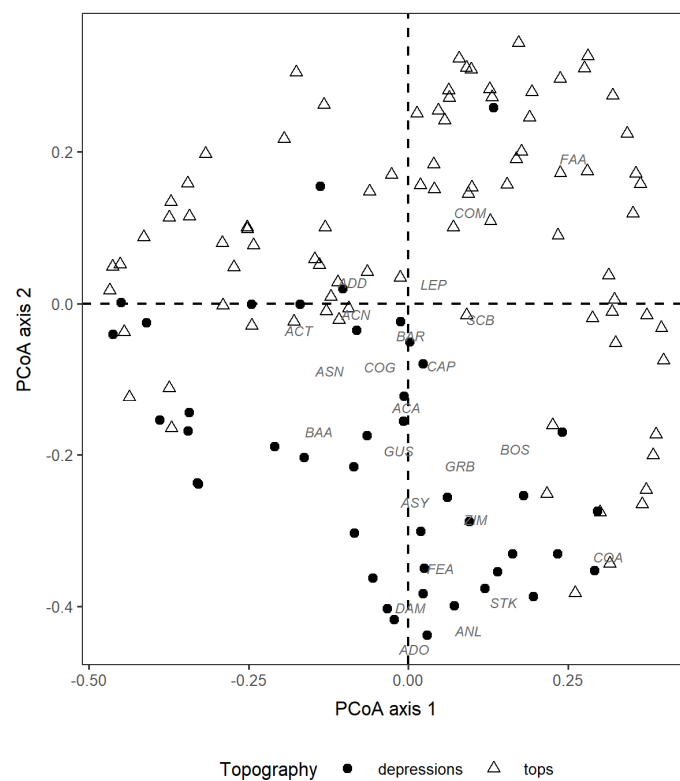


Figure 4.2 – Principal Coordinates Analysis on the 139 plots. Plots are represented by squares (for the depressions) and triangles (for the tops). Species are displayed by a three letters acronym (see Table 4.1).

¹³ These results were not part of the paper published in Journal of Arid Environment. They are however part of this manuscript and can be consulted in section 4.6, Figure 4.10.

Topography also has a clear impact on the species richness, the woody cover and the density of adults, saplings and seedlings (Figure 4.3) as confirmed by mean comparisons ($P < 0.05$). Tree mortality¹⁴ is the only studied variable that shows no difference relative to the topographic element, with a rate of 10.5% for tops and depressions. The plots located inside depressions present a mean specific richness of 4.5 versus 2.4 for the tops. Adult trees are present at a mean density of 157.5 ind.ha⁻¹ in the depressions (35.3 on the tops) and saplings at 155.2 (38 on the hilltops). Woody cover inside depressions reaches 25% against 5% on tops. As a reminder, the woody cover does not reflect the actual fraction of soil covered by vegetation, as the overlapping crowns were not identified. As far as macro relief is concerned, the saplings density in the plains depressions is higher than in the dunes depressions and the adult density on plains hilltops is also higher than on the dunes hilltops (data not shown).

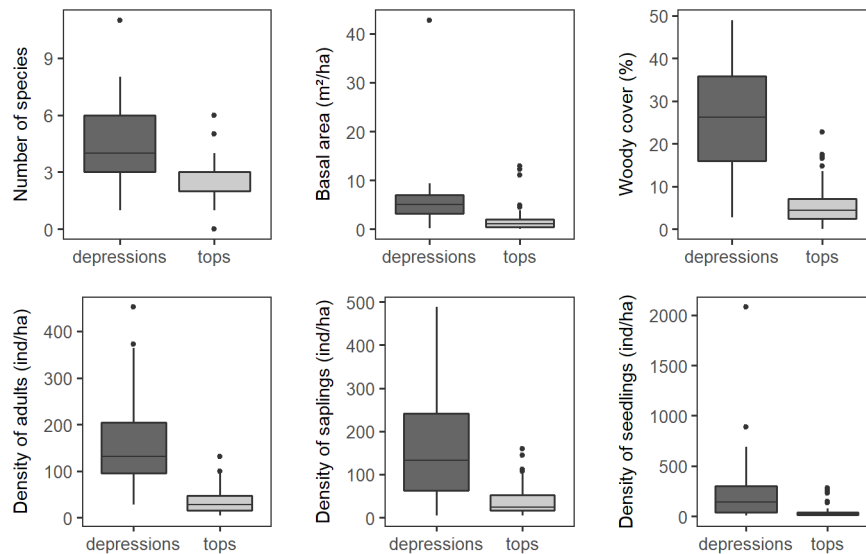


Figure 4.3 – Specific richness, basal area, woody cover, density of adults, saplings and seedlings for the two topographic elements. The boxplots show the median and the 25th and 75th percentiles; the open circles represent outliers.

¹⁴ « Dead woody plant » would be a more appropriate term, as the numbers come from a single inventory and do not reflect an actual rate (number of dead plants per year).

At the species scale, the majority of the stand is occupied by three species: *Balanites*, *Boscia* and *Calotropis* (Table 4.1). Far behind are the secondary species such as *Sclerocarya birrea* and *Acacia tortilis* for the hilltops, with densities of 2.7 and 1.6 ind.ha⁻¹ whereas in depressions, *Grewia bicolor* (4.2 ind.ha⁻¹) is often found, along with *Acacia seyal* (3.9 ind.ha⁻¹). However, the order of species importance is different when it comes to crown cover and frequency (i.e. the proportion of plots in which the species was recorded, Table 4.1). The most common species in frequency are also *Balanites* and *Boscia*, which were encountered in more than 50% of the plots. However, and despite its low density, *Sclerocarya* is quite frequent and was recorded in nearly one plot out of two. It also comes in first place on hilltops given its high cover of 176 m².ha⁻¹ and in second place in depressions with 352 m².ha⁻¹. *Calotropis* has a lower frequency, with 21.9% on tops and 44.2% in depressions, which means that when this species is present, it is with a high density. *Acacia tortilis* is also common (frequency of 37.2% and 20.8%) though its densities are low.

Figure 4.4 allows the comparison of population structures with the four indicators (slope, mean quotient between successive classes, permutation index and Simpson's index of dominance) for seven species. It should be remembered that the number of plots inventoried in depressions and on tops are not the same. It is therefore the general shape of the distributions that have to be compared and not the total number of individuals. Two species, *Sclerocarya* and *Grewia* present an absence of saplings despite the numerous seedlings. This indicates a failure of seedlings to establish. Two species, *Balanites* and *Acacia seyal* present a particularly high number of seedlings (>200), generally found in clusters of several square meters.

Linear regressions on size classes show that all species on the tops have a negative slope, which indicates a relatively good recruitment, depending on the slope steepness. *Balanites* has the steepest slope and therefore presents a higher regeneration capacity than the other species. Inside the depressions, *Sclerocarya* is the only species to show a positive slope, a sign of a poor recruitment.

The instability of the four species population on hilltops is emphasized by the standard deviations of the mean quotients, which are all higher than the means themselves, indicating a discontinuity between size classes. The only exception is *Balanites* whose population is the only one that appears to be quite stable. In depressions, the populations of *Acacia seyal*, *Acacia tortilis* and *Grewia* also present high standard deviation of mean quotient. *Balanites*, *Acacia senegal* and *Acacia tortilis* (for the tops only) show relatively small permutation indices, meaning that those

populations are close enough to an “ideal” population for which the size class would decrease in a monotonous way. *Grewia* and *Sclerocarya* are the only species presenting a Simpson’s index of dominance lower than 0.1. The size classes of their population are thus distributed rather evenly. However, the high permutation indices for those two species indicate that their population structures remain distant from the negative exponential structure.

Regarding deep well distance, the models (results not showed) do not highlight any influence on the studied variables ($P > 0.05$ for specific richness for adults and saplings, densities for adults, saplings and seedlings, basal area and woody cover). Among the eight species ratio, the *Acacia tortilis* ratio on tops is significantly ($P < 0.01$) affected by the remoteness of deep wells and decreases with distance.

4.3.2. Regeneration features

Among the 23 species inventoried at the adult stage in the 70 sub-sampled plots (*Bauhinia*, which was found in one of the 139 plots, was not recorded in the subsampling), seedlings and/or saplings (i.e. regeneration) was found for 19 of them. Indeed, the species *Acacia ataxacantha*, *Adenium*, *Anogeissus*, *Dalbergia* and *Faidherbia* are completely absent in the regeneration class. For five species (*Acacia nilotica*, *Combretum glutinosum*, *Commiphora africana* (A. Rich.) Engl., *Leptadenia pyrotechnica*, *Stereospermum*), the number of regenerations was very low with less than ten individuals for seedlings and saplings taken together. Moreover, despite their presence in the seedling stage, no saplings were found for *Acacia nilotica*, *Bauhinia*, *Combretum glutinosum*, *Commiphora*, *Grewia*, *Sclerocarya* and *Stereospermum*. The more abundant species in sapling stage are, by alphabetical order, *Acacia tortilis*, *Balanites*, *Boscia*, and *Calotropis* with densities between 2 ind.ha⁻¹ (*Acacia tortilis*) and 50 ind.ha⁻¹ (*Boscia*).

The regeneration rates for the saplings are of 48.2% in the depressions and 54% on the hilltops whereas the seedlings have a rate of 61.5% in the depressions and 50.4% on the tops. Table 4.2 gathers the regeneration rates for the species for which more than five adults were inventoried. The species are clustered into four groups according to their presence on one or both topographic elements and the abundance of their regeneration. The first group includes *Acacia senegal*, *Acacia tortilis*, *Balanites*, *Boscia* and *Calotropis*. These species are well represented on both topographic elements (although the *Acacia senegal* densities are lower) and their regeneration (saplings and seedlings) reflects this distribution pattern, with good regeneration rates in depressions and on the tops. *Acacia seyal*, *Guiera* and *Ziziphus*,

species that are mainly found in the depressions at all growth stages, compose the second group. *Grewia* and *Sclerocarya* illustrate the third group, which shows a lack of saplings even though the seedling rates are greater than 70%. This trend has already been seen in Figure 4.4. *Combretum glutinosum* is the only species of the fourth group. The species is already scarce at the adult phase and the regeneration rates are close to zero.

Table 4.2 – Regeneration rates of seedlings and saplings and the corresponding density of adults in the 70 sub-sampled plots. The species for which less than five adults were inventoried (*Acacia nilotica*, *Adansonia*, *Bauhinia*, *Combretum aculeatum*, *Commiphora*, *Feretia*, *Leptadenia pyrotechnica* and *Stereospermum*) are not shown. The groups refer to the presence of species on the two topographic elements (D: depressions; T: tops) and to the abundance of the regeneration.

Species	Density of adults (ind.ha ⁻¹)		Seedlings rate (%)		Saplings rate (%)	
	D	T	D	T	D	T
Group 1						
<i>Acacia senegal</i>	1.5	0.2	60.0	40.0	33.3	25.0
<i>Acacia tortilis</i>	3	0.7	69.2	63.0	50.0	66.7
<i>Balanites aegyptiaca</i>	65.7	4.7	64.0	64.0	36.8	32.3
<i>Boscia senegalensis</i>	108.5	17.5	37.6	44.3	57.4	50.5
<i>Calotropis procera</i>	40	3.3	28.6	23.7	40.5	59.5
Group 2						
<i>Acacia seyal</i>	6.5	0.1	92.7	0	35.8	0
<i>Guiera senegalensis</i>	4.25	0.5	71.2	0	45.2	0
<i>Ziziphus mauritiana</i>	2.2	0	83.6	0	25.0	0
Group 3						
<i>Grewia bicolor</i>	8.2	0.3	76.4	76.5	0	0
<i>Sclerocarya birrea</i>	5.7	3.3	85.0	64.8	0	0
Group 4						
<i>Combretum glutinosum</i>	0.7	0.4	0	14.3	0	0

The position of saplings and seedlings relative to the crowns (Figure 4.5) shows that the majority of the seedlings (77%) are found under a crown except for *Balanites* which has its seedlings distributed nearly equally between the cover and the outside. For the saplings, the trend is less clear as most of *Acacia tortilis* and *Acacia seyal* saplings are outside the canopy but *Guiera* and *Feretia* are not. As for *Balanites* saplings, the proportion is rather balanced between the two positions.

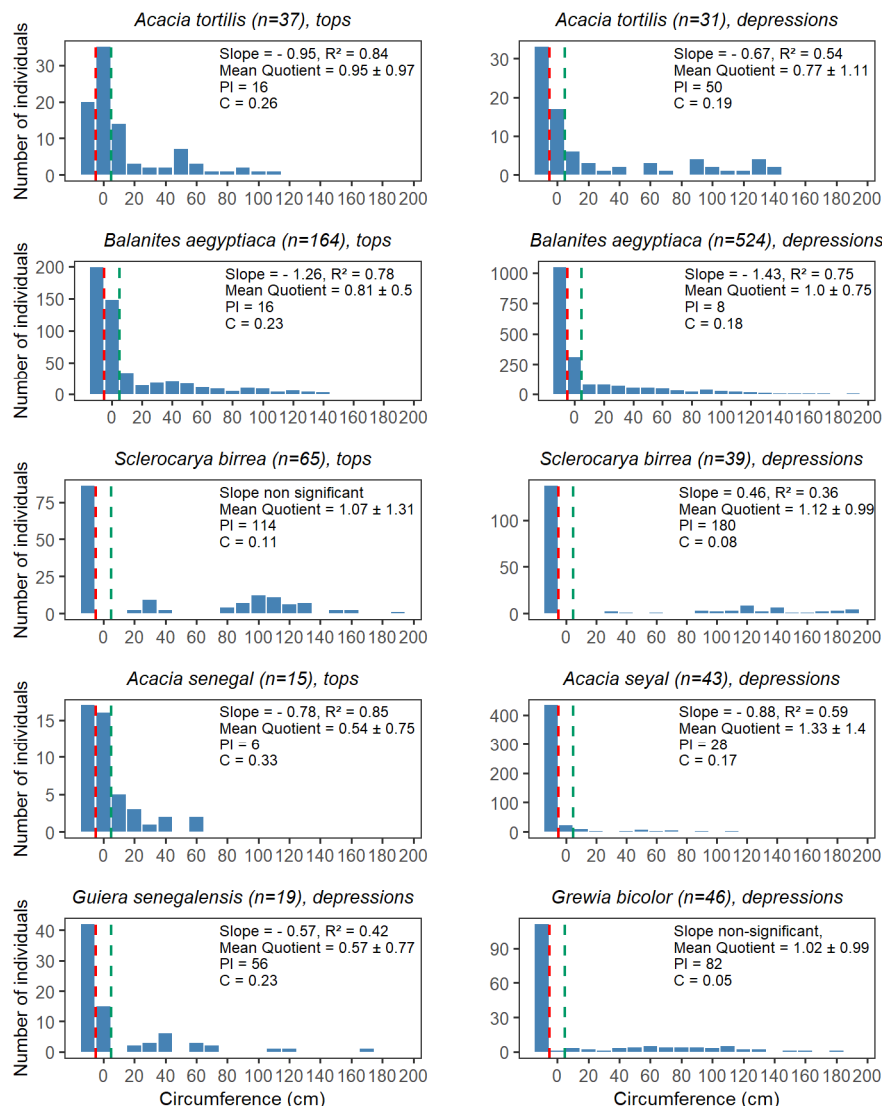


Figure 4.4 – Size Class Distribution analysis: population structures of four species on the tops and six species in depressions. The horizontal line separates the species that are found on the two topographic elements (*Acacia tortilis*, *Balanites*, *Sclerocarya*) from the others. On each graph, the vertical red dotted line highlights the transition from the seedlings (counted in the 139 plots), to the saplings (the first class: 0-10 cm) and therefore represents the threshold above which we consider the regeneration stable and as part of the tree stand. The vertical green dotted line separates the saplings from the rest of the stand. For each species, the slope ($P < 0.01$ unless stated otherwise) and the R^2 of the linear regression; the mean quotient and its standard deviation; the permutation index (PI); and Simpson's index of dominance (C) are indicated. The number of individuals (n) per species is indicated between brackets.

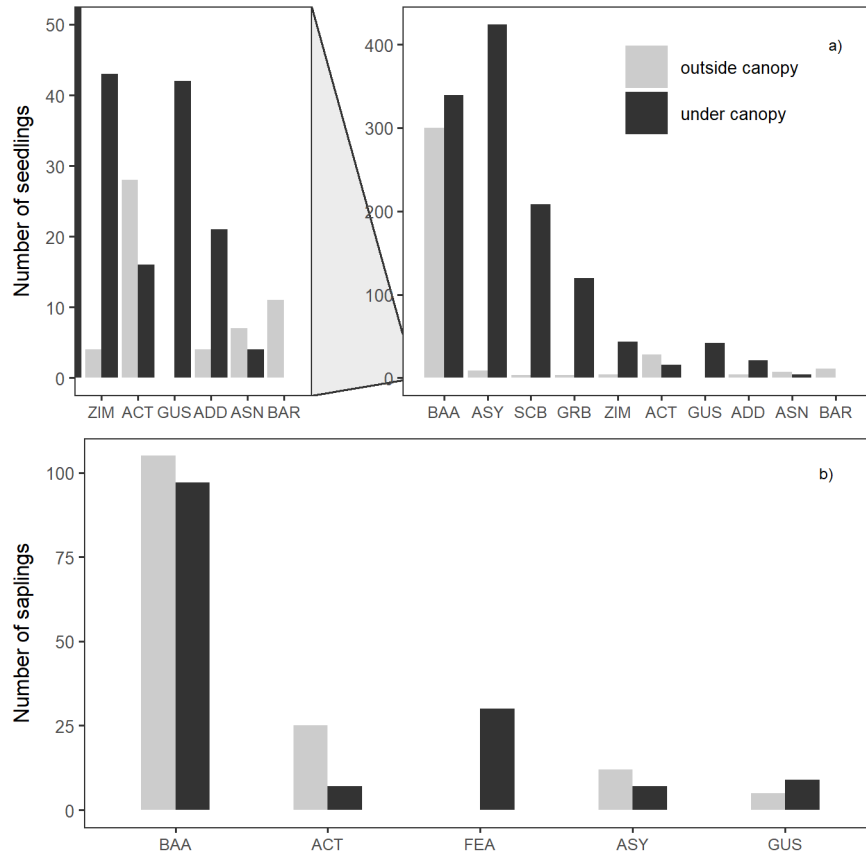


Figure 4.5 – Number of a) seedlings, with a zoom for species having a number of seedlings below 50, and b) saplings located under and outside the canopy cover (for the species with more than ten individuals). The three letters code are referring to species (see Table 4.1).

For each species, we looked into the average distances between its seedlings and the nearest adult (from any species or from the same species, Figure 4.6) in order to investigate how close to the adults the seedlings are located. According to the pairwise comparisons using Wilcoxon rank test, *Grewia* seedlings are located at a significantly ($P < 0.05$) smaller distance (0.9 ± 0.9 m) from an adult of any species than the seedlings of *Acacia seyal* (3.1 ± 1.8 m), *Acacia tortilis* (4.1 ± 3.9 m), *Adansonia* (4.5 ± 4.8 m) and *Balanites* (3.4 ± 2.9 m). *Sclerocarya* seedlings are also located at a significantly ($P < 0.05$) smaller distance (1.9 ± 1.3 m) than the seedlings of *Acacia seyal* (3.1 ± 1.8 m). Regarding the distance with individuals of

the same species, the only significant difference (to the alpha threshold of 5%) is between *Balanites* (8.7 ± 10.9 m) and *Acacia tortilis* (23.7 ± 11.8 m).

We can distinguish two groups of species according to the proximity to their supposed parents (Figure 4.6). The first group includes the species with an average distance from the nearest adult of the same species above 10 m and much greater than the average distance to the nearest adult of any species. This is the case for *Acacia tortilis*, *Acacia senegal*, *Bauhinia* and *Grewia*, for which more than 95% of the seedlings are found far away from their likely parents. *Adansonia*, *Acacia seyal*, *Balanites*, *Guiera* and *Sclerocarya* have their seedlings at less than 10 m for their likely parent and form the second group. *Ziziphus* seedlings are intermediate, with an average distance from the adult of the same species of less than 10 m but with a large variability around this average.

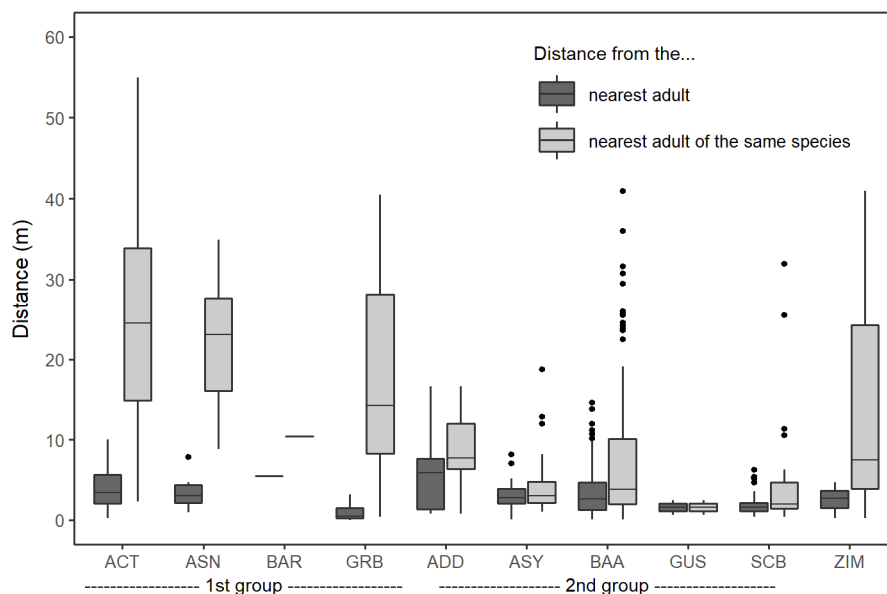


Figure 4.6 – Average distances between seedlings of a given species and the nearest adult of any species (dark grey) and of the same species (light grey). The species represented here are those with more than ten seedlings.

The “hosting indices” of the different species are indicated in Table 4.3. The mean distance to the seedlings and the mean crown radius of the adults are also given to evaluate if the seedlings are in the shade of the adult trees. The species presenting the higher indices (*Acacia seyal*, *Ziziphus*, *Sclerocarya* and *Adansonia*) are

all trees compared to shrubs like *Boscia* and *Calotropis*, which have lower values. The *Balanites* and *Acacia senegal* trees also have a relatively high index. If we look at the mean biometric parameters (Appendix B¹⁵) of the closest adults for each species of seedling, this allows us to examine in greater detail the size of the trees and hence, the shadow offered by the adults. Considering that above 3 m height, we are dealing with trees rather than bushes, 12 species out of 16 in the seedling phase are located near relatively tall trees, with crown diameters mostly larger than 4 m, which offer a cover of approximately 20 m². For the four remaining species, the number of counted seedlings is low (less than ten individuals) so any conclusions about these parameters is difficult.

Table 4.3 – Assessment of the “hosting ability” of the adults on the 70 sub-sampled plots. The number of adults inventoried on the 70 plots are between the brackets and the star indicates if the species biological form is the one of a tree (by opposition to bushes and shrubs).

Adult species	Number of seedlings the closest to that species	Mean distance to the seedlings (m)	Mean radius of the species crown (m)	Hosting index
<i>Boscia senegalensis</i> (702)	147	2.9	0.98	0.21
<i>Combretum glutinosum</i> (9) *	2	0.9	3.55	0.22
<i>Calotropis procera</i> (205)	67	2.5	0.93	0.33
<i>Acacia tortilis</i> (22) *	8	1.3	3.56	0.36
<i>Grewia bicolor</i> (38)	14	2.2	2.9	0.37
<i>Feretia apodanthera</i> (3)	2	1.5	1.18	0.67
<i>Acacia senegal</i> (9) *	8	1.8	3.14	0.89
<i>Balanites aegyptiaca</i> (363) *	489	2.9	2.09	1.35
<i>Guiera senegalensis</i> (24)	47	1.5	2.72	1.96
<i>Combretum aculeatum</i> (1)	2	1.7	3.1	2
<i>Adansonia digitata</i> (3) *	10	8.3	5.96	3.33
<i>Sclerocarya birrea</i> (67) *	290	2.5	4.97	4.33

4.4. Discussion

4.4.1. Influence of environmental factors

The species richness observed inside the study area (24 species) is in line with the studies of Poupon (1980) and Vincke *et al.* (2010) who respectively recorded 28

¹⁵ Appendix 16 in this document.

(included 3 lianas) and 22 woody species in the sandy Ferlo. However, the density (42.5 ind.ha^{-1}) is much lower than that found by Poupon (1980) 847 ind.ha^{-1} . It is the same with the study of Ndiaye *et al.* (2014), who observed a density of $172.8 \text{ ind.ha}^{-1}$ and a woody cover of 20.1% in Widou Thiengoly. These higher numbers could be explained by the differences in the sampling methodology, Ndiaye *et al.* (2014) applied a random sampling and Poupon (1980) inventoried the vegetation inside a quadrat protected by a fence.

Our first hypothesis regarding the impact of topography is supported by the results of the PCoA and the mean comparisons tests. Topography strongly influences the specific richness, the densities of adults, seedlings and saplings, the basal area and the woody cover, which all are significantly higher in depressions. Botanical composition, as shown by the Principal Coordinates Analysis, is also influenced, with the presence of some species being mostly related to the topographic position (e.g. *Acacia seyal*, *Grewia bicolor* and *Ziziphus mauritiana* in depressions).

These results are in line with the work of Poupon (1980) in Fété-Olé where the tree density was ten times higher in depressions than on the hilltops and the basal area $0.6 \text{ m}^2.\text{ha}^{-1}$ compared with $8.8 \text{ m}^2.\text{ha}^{-1}$ in the depressions. Cornet (1992), using the same site as Poupon, observed an increase in the woody vegetation density in depressions while the density declined on hilltops, which indicates a well-marked difference between the two topographic elements. In the lateritic part of the Ferlo, de Wispelaere (1980) has described the same process in the neighborhood of a deep well, between 1974 and 1978, using aerial photos analysis.

The greater water availability in the depressions, due to water run-off and a higher clay ratio (Cornet, 1992), is most likely the main factor explaining these differences in structure and composition of woody vegetation. However, the topographic position probably also reflects the influence of other factors such as the nitrogen and phosphorus soil content that are potentially higher in the depressions, as a consequence of the greater input of animal feces near the temporary ponds or below the canopy where animals look for shade to rest (Pierre Hiernaux, personal communication). As for the macro relief effect on adult and sapling density, it is likely an effect of soil type.

Our second hypothesis assumed that we would find an increase in density and species richness in the plots located away from the deep wells. This is not the case as the only variable impacted by deep well distance is the *Acacia tortilis* ratio on hilltops, which presents a decreasing trend when we move away from the deep

wells. Tybirk (1991) stated that the germination of this species often occurs in animal feces. The accumulation of excretions near deep wells could explain this result. The Principal Coordinates Analysis does not reveal a significant effect of the deep well distance on the botanical composition.

To our knowledge, apart from Vincke *et al.* (2010), this is one of the first studies dealing with the location of deep wells and the impacts on woody vegetation using field inventory in Senegal. Through aerial photos, de Wispelaere (1980) showed that patches of bare area were mostly present between 3 to 6 km around the deep well of Revane in the lateritic Ferlo whereas Hanan *et al.* (1991) who studied the primary production through NDVI around 20 deep wells in Senegal found no significant relationship with the deep well proximity. In Mali, Dembélé *et al.* (2006) observed through a field inventory a regeneration gradient when moving away from permanent water points.

Our second hypothesis is invalidated, as the effect of deep well location is not marked on the studied woody vegetation variables. However, we cannot conclude that the anthropic pressure has no effect on woody vegetation from 2 km up to 15 km from the deep wells. Indeed, the descriptor used to assess the anthropic pressure (i.e. the distance from the nearest deep well) does not cover all the sources of anthropic activities such as temporary ponds and Fulani camps (0.45 camps.km⁻² inside the two circular areas of 15 km radius; Appendix C¹⁶). Although the sampling of our inventory plots attempted to avoid the influence of the camps with a buffer of 500 m, they still could generate micro-gradients of pressure that could mask the influence of deep wells distance. Nevertheless, taking into account the deep well remoteness in our sampling design as a potential factor influencing the woody vegetation, has strengthened the results regarding the effects of the topography.

4.4.2. Population structure and regenerative capacity

The size class analysis reveals that most of the species present an unstable population as indicated by the high standard deviations for the mean quotient between the individuals of successive classes. Besides, their structures are far from the negative exponential population structure as expressed by their high permutation indices. They also present an uneven repartition of the individuals between classes as shown by the high Simpson's indices of dominance. Moreover, these analyses couldn't be done for all the species due to lack of

¹⁶ Appendix 9 in this document.

individuals so it should also be a sign, for those species, that their population dynamics is far from the theoretical ideal population structure and that their persistence in the study area is uncertain. Our starting hypothesis about having more stable and balanced populations with a better distribution of individuals per size class in depressions is not confirmed for the three species that were analyzed on both topographic elements (*Acacia tortilis*, *Balanites*, *Sclerocarya*).

As a comparison, the study of *Balanites* and *Acacia seyal* populations from Sop *et al.* (2011) in the south Sahel in Burkina Faso gives values for the permutation index between zero and two. These large differences with our data are probably due to the lack of individuals for some species. Indeed, average densities recorded in Burkina vary from 291 to 560 ind.ha⁻¹ compared to our plots where densities are 157 ind.ha⁻¹ in depressions and only 35 ind.ha⁻¹ on tops. The PI values obtained here are closer to those observed by Wiegand *et al.* (2000) on population of *Acacia tortilis* in the Negev desert (Israel) where the annual rainfall is 38 mm (PI between 14 and 60).

The variability of the relationship age-circumference, which is not the same for all the species, could be seen as a limitation of the size class analysis. This relation for a given species could also vary due to several factors such as water availability, soil type, browsing pressure and the common pruning or cutting practices for wood or fodder.

Among the 19 species encountered in the seedlings or saplings phases, five of them count less than ten individuals and 12 are not well represented in the saplings class, with less than ten individuals or none at all. For the species *Sclerocarya* and *Grewia*, no saplings were found, even though the adult trees and the seedlings are quite numerous. The size class analysis also reveals for these species a lack of “young” individuals (with a small circumference). The lack of saplings and young trees raises concern about the persistence of these two species. The situation is also critical for *Combretum glutinosum*, as the seedlings are not abundant and saplings non-existent. This situation is not new, as Miehe (1994) already observed the lack of saplings for *Sclerocarya* and *Combretum glutinosum* in Widou Thiengoly and the dominance of *Balanites* among the regenerations. She also noted that *Boscia*, *Balanites* and *Acacia tortilis* are regenerating even under a high grazing intensity. Nevertheless, cohort phenomenon could compensate for this lack of regeneration (i.e. seedlings that successfully develop in some favorable years) which could be a strategy for species like *Acacia seyal*, *Acacia senegal*, *Acacia tortilis* and *Combretum glutinosum* (Pierre Hiernaux, personal communication).

The trends that we observed with the Size Class Distribution analysis and the regeneration confirm previous observations in this zone. Indeed, Miehe (2002) stated that the tree stands of *Sclerocarya* and *Combretum glutinosum* were declining and without regeneration. She also observed a decrease in *Acacia senegal* and *Acacia seyal* populations along with an increase of drought resistant species like *Acacia tortilis* and *Boscia*. She pointed to these two latter trends as an indicator of rainfall shortage.

Natural regeneration has rarely been investigated in detail and, to our knowledge, there are very few studies about soil seed banks, regeneration mechanisms and ecological requirements of seedlings and saplings in arid zones (Argaw *et al.*, 1999; Wilson and Witkowski, 1998; Witkowski and Garner, 2000) and more specifically in the Sahel. This lack of data limits the interpretation of our results. Despite these limitations, our exploratory study can be seen as a first attempt to understand the regeneration distribution patterns with respect to the adult location, the topography, regardless of the regeneration mechanism.

The positive effects of woody cover on seedlings is clear, as 77% of the seedlings were found under a crown. Tybirk (1991) states that water, which is linked to soil type and light exposure, is the most important factor for the survival and growth of the regeneration. We can assume that below the canopy, the water availability is higher, thanks to the reduction of the temperature and of the sun radiation, as demonstrated by Akpo *et al.* (2005) in Souilène (Senegal). For example, the majority of *Acacia seyal* seedlings (98%) are found under the canopy and this species is known to be very sensitive to water supply (Tybirk, 1991) and requires shade to develop (Joker, 2000b). However, when it comes to saplings, the results are more heterogeneous and the small number of individuals does not allow us to draw conclusions.

Besides the distribution of saplings and seedlings under or outside canopy cover, we highlighted the important role of tree growth form compared to shrubs. Indeed, the three species that are hosting the highest number of seedlings under their crowns are *Acacia seyal*, *Ziziphus* and *Sclerocarya*. The low index of tree *Combretum glutinosum* might be due to its very sparse crown (Arbonnier, 2009). However, the index value for *Acacia tortilis* is odd given its growth form and dense crown. This finding is in contradiction to Akpo and Grouzis (1996) who have reported a positive effect of the *Acacia tortilis* cover for the woody regeneration in the Ferlo. The other peculiar result is for *Guiera*, which showed a high index for a bush. Its shape and mean height of 4.1 m make it appear to be a small tree but it has very similar features to *Grewia*, which has a much lower index.

The analysis of the distance between the seedlings and the nearest adult from the same species reveals two groups of seedling behavior. The first group has most of their seedlings located near the adult of the same species (*Acacia seyal*, *Balanites*, *Guiera*, *Sclerocarya*, and *Ziziphus*) whereas seedlings of the second group are mostly found far away from the adults in the species *Acacia tortilis*, *Bauhinia*, *Combretum aculeatum*, and *Grewia*. This could be linked to both their dispersal mode and/or their regeneration mechanisms. Three species of the first group (*Balanites*, *Sclerocarya*, and *Ziziphus*) are dispersed mostly by zoochory (Helm *et al.*, 2011; Royal Botanic Gardens Kew, 1999); however, they have heavy seeds, which fall directly to the ground beneath the tree. This could explain why they are found near the parents. *Guiera* is supposed to be dispersed by wind (Dukku, 2010) so it is rather peculiar that seedlings are found directly under a parent tree. Birds are the principal dispersal agent for *Acacia seyal* (Tybirk, 1991) so seeds might travel long distances. The species of the second group are mostly dispersed by zoochory, either by cattle (*Acacia tortilis*, *Acacia seyal*, *Bauhinia* and as a secondary agent for *Acacia senegal*, the first one being the wind, (Tybirk, 1991) or by birds (*Grewia*) except for *Combretum aculeatum*, which is probably wind dispersed (Steentoft, 1988).

Regeneration mechanisms (true seedling, coppice, root sucker...) are also acting on the spatial distribution of the seedlings. For tree species in semi-arid savannas the relative proportion depends on the species, the disturbance regime, the climate and the site conditions (topography for instance) (Bellefontaine, 1997; Ky-Dembele *et al.*, 2007). Regarding the species encountered in our study area, most of them have the ability to reproduce by vegetative propagation (Bellefontaine, 1997). While the ratio between this regeneration mechanism and true seedlings is unknown for most of the species, Argaw *et al.* (1999) mention that *Acacia senegal* mostly propagates by direct seedlings; *Acacia seyal* and *Acacia tortilis* by direct seedling and coppicing; and *Balanites* uses direct seedling, coppice and root suckers.

As the amounts of *Balanites* saplings under and outside canopy are equivalent, and that Schmidt and Joker (2000) state that this species is intolerant to shade after the seedling stage, we can assume that this result reflects the presence of root suckers under the canopy. Indeed, root suckers have access to more resources than a young plant coming from seed. This capacity to regenerate through multiple mechanisms gives *Balanites* a competitive advantage, particularly in the case of disturbances.

Still, as we counted regeneration for a single year, our results have to be interpreted with caution. While keeping in mind that we don't know the origin of the seedlings counted, the inter-annual variability of the seeds production is high as mentioned by Poupon (1980). In Fété-Olé in the north Ferlo, he found that in 1972, a very dry year, the fructification only occurred for *Boscia*. Moreover, the number of seedlings depends on the seed production of that year and on the several previous years, as seeds remain dormant. For woody legumes, the existence of a seed banks is often assumed although few studies have focused on this (Tybirk, 1991). Germination is also a very variable phenomenon. Following the 1972 drought in Fete-Ole, Poupon (1980) observed three types of pattern regarding the germination rate: (i) species with a demographic explosion and whose germination rates are high every year (*Balanites*, *Boscia*, *Guiera*); (ii) species with a demographic explosion but not every year (*Commiphora*, *Acacia senegal*); (iii) species with a very low germination rate (*Grewia*). But the saplings inventory confirms the trend observed regarding seedlings, as they are not dependent on the conditions of a single year and are therefore more reliable for making assumptions about the future of species (Miehe, 1994). The size class analysis also allowed us to study, for some species, their population dynamics as discussed further.

4.4.3. Persistence of woody plant population

Species can be classified in four groups according to three parameters: (i) their frequency and density in the current woody stand; (ii) the abundance of their regeneration and their population stability (based on size class analysis); and (iii) their ecological role for seedlings (based on the hosting index). The first group includes species with a high frequency, a stable population and a good hosting index for regeneration: *Balanites* on hilltops and in depressions, *Acacia seyal* in depressions and to a lesser extent *Guiera* in depressions. The second group is composed of species with a high frequency, a secured regeneration, but with poor ability to host seedlings: *Boscia* and *Calotropis*. The third group includes species with an average frequency and a high ecological interest but with unstable populations and few regenerations: *Sclerocarya* on hilltops and depressions, *Grewia* in depressions and *Ziziphus* in depressions. Finally, we have other species with lower frequency and/or poor effect on regeneration: *Acacia senegal*, *Combretum glutinosum*.

It should be kept in mind that half of the species inventoried, *Acacia nilotica* or *Adansonia* for instance, cannot be included in these four groups given their

scarcity. They are also threatened, as they do not have saplings to ensure the persistence of their populations. A rise in the proportion of group 2 compared to group 3 would put the persistence of woody vegetation at risk in the long term and would completely change the vegetation structure from a wooded savanna to a shrubby savanna.

A particular attention should be paid to the areas located in depressions. Indeed, they host a higher number of species than the hilltops, potentially ensuring a higher resilience. Besides, these microsites are places highly favorable for regeneration for two reasons. Firstly, depressions could be a refuge for regeneration during the years where there is a large gap between two rainy episodes. As stated by Tybirk (1991), the soil in these depressions is humid for a longer period and it gives more time for the seedlings to develop roots that reach a soil layer permanently humid. Secondly, depressions are the preferential habitat of some key species like *Acacia seyal* and *Grewia* (group 3). The importance of protecting these depressions is reinforced by the fact that they represent only 6% of the whole study area as mentioned in section 4.2.2.

4.5. Conclusion

In an area of about 1400 km² around two deep wells in the northern Ferlo, the topography was determined to be the environmental factor having the most significant effect on the woody plant population parameters and the botanical composition. The impact of topography is far greater than the effects of soil type or the proximity to deep wells. Regarding the impacts of the anthropic pressures on these ecosystems, we suggest that remoteness from deep wells beyond 2 km is not the appropriate descriptor to use, considering the distribution of temporary ponds and Fulani camps.

We have highlighted the uncertain future of several tree populations (*Sclerocarya*, *Combretum glutinosum*) as a result of a size class analysis. Only three species have an equilibrated and stable population (*Acacia tortilis*, *Acacia senegal*, *Balanites*). This observation is quite alarming given the positive effect of large trees on regeneration. The shrubs, *Boscia* and *Calotropis*, are also well represented at the regeneration stage and the adult stage. The rest of the species are only encountered as isolated individuals with little or no regeneration.

Topography is a key factor for woody vegetation and the depressions sites seem to guarantee a certain resilience of these ecosystems with a more abundant pool of tree species than the hilltops along with a higher density of adults and

regeneration. Still, to strengthen our knowledge of the resilience of these ecosystems, relevant indicators should be monitored over several consecutive years (regeneration ability for instance). Our data are unique for this area regarding the type of indicators used and bring a complementary perspective to the remote sensing studies by offering data at the species scale. In the future, if some management plan should be implemented, we suggest that a deeper study of the impact of depressions with a consideration of the functional role of species should be one of the key factors in addition to socio-economic considerations.

4.6. Complementary analyses

The present section gathers analyses that were not integrated in the paper of Dendoncker and Vincke (2020) though they rely on the same field sampling presented in section 4.2.2.

4.6.1. Methodology

For each species, the Importance Value Index (IVI) was computed (Curtis, 1959). This index is a way to express the ecological importance of a species within a vegetation community by adding the relative dominance (Dom_r), the relative density (D_r) and the relative frequency (F_r) of the species. This quantity is then divided by three to express the IVI in percent, a value of 0% indicates an absence of dominance among the species and a value of 100% translates a single dominance.

The relative frequency (F_r) of a species is the ratio between the frequency of this species (F_i , i.e. the percentage of plots in which the species is counted) and the sum of the frequencies of all species ($\sum F_i$).

$$F_r = \frac{F_i}{\sum F_i} \times 100$$

The relative density of a species (D_r) is the ratio between the number of individuals of the considered species, N_i , and the total of individuals, N .

$$D_r = \frac{N_i}{N} \times 100$$

The relative dominance of a species (Dom_r) is the ratio between the crown cover of the species, R_i , in square meters and the total woody cover of the tree stand, R .

$$Dom_r = \frac{R_i}{R} \times 100$$

In addition to the IVI, we performed supplementary analysis on the PCoA realized in section 4.2.3.1. We tested the influence of relief and the interaction between topography and relief on the botanical composition with Anova. Finally, we performed an additional PCoA on the saplings communities, following the same methodology.

4.6.2. Results and discussion

The three IVI components, relative density, relative dominance and relative frequency are represented in Figure 4.7 for both topographic elements. The species *Boscia* and *Balanites* occupy the first positions regarding their relative density and their relative frequency on both topographic elements. The case of *Sclerocarya* is interesting to consider. Its relative density puts it in fourth position. However, regarding its relative dominance, it takes the first position on tops, before *Balanites*, and the second one in depressions. *Sclerocarya* is also in third position for the relative frequency. Briefly, we are dealing with a species that though is rare in density, is found in many plots (relative frequency) and presents large crowns (relative dominance). This status can be important to consider regarding the effects of this species on ecosystem functioning and thus on the provision of ecosystem services.

The Importance Value Index per species on each topographic element is represented in Figure 4.8. In depressions, it is clear that both *Balanites* and *Boscia* are the most important species with IVI values of 29 and 22%, respectively. On tops, these two species are accompanied with *Sclerocarya* with an IVI of 19%. *Calotropis*, which was well represented in terms of densities, now comes in third place in depressions (IVI = 8.9%) and in fifth place on tops (IVI = 6.4%), behind *Acacia tortilis* (IVI = 7.3%).

The Principal Coordinates Analysis carried out on the adults and on the saplings set revealed no influence of the relief on both axes (Figure 4.9 and Figure 4.10). The top panel of Figure 4.9 is the replicate of Figure 4.2 but serves as comparison for the bottom panel that illustrates the two relief categories. However, the influence of local topography is outlined for the saplings, as it was for the adults (section 4.3.1). Indeed, depressions and tops are mostly separated by the second axis, depressions being located on the top of the plot (Figure 4.10).

4.6.3. Partial conclusion

The computation of the Importance Value Index showed another perspective of the species abundances in woody vegetation compared to the simple density analysis. The ecological importance of *Sclerocarya birrea* was highlighted, particularly on tops where it occupies the third position in the IVI ranking. The Principal Coordinates Analysis on the saplings confirmed the effect of topography on the botanical composition of saplings communities.

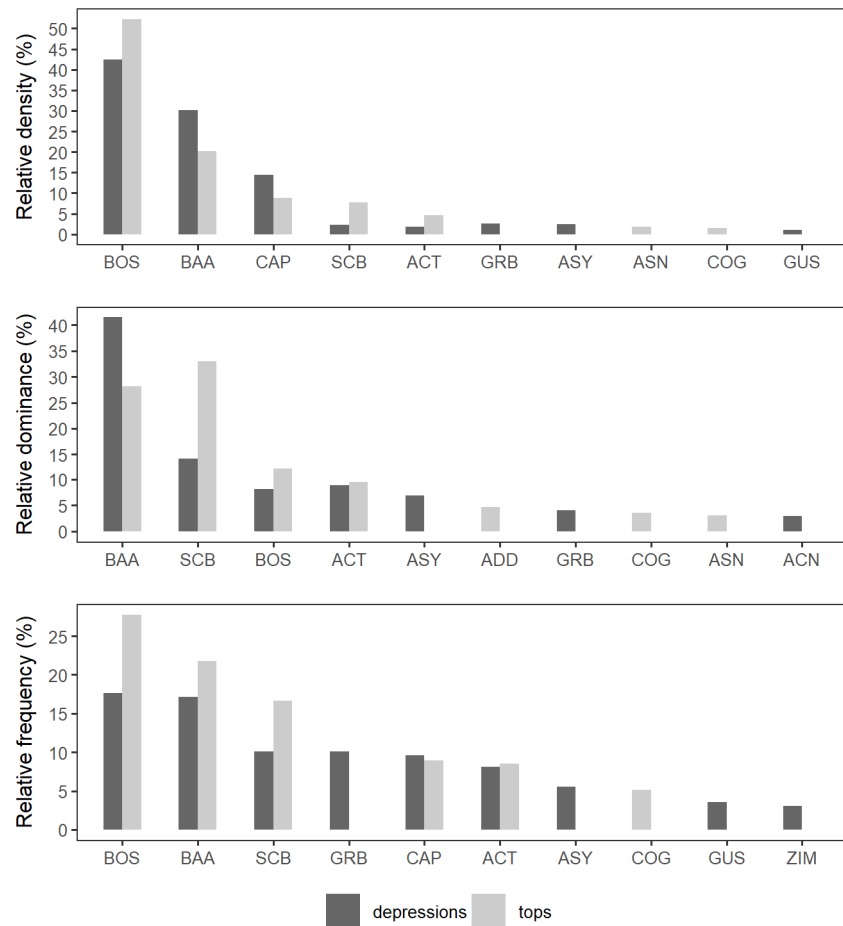


Figure 4.7 – Species IVI components according to the topography: relative density, relative dominance (based on woody cover values) and relative frequency. Only the ten highest values are represented.

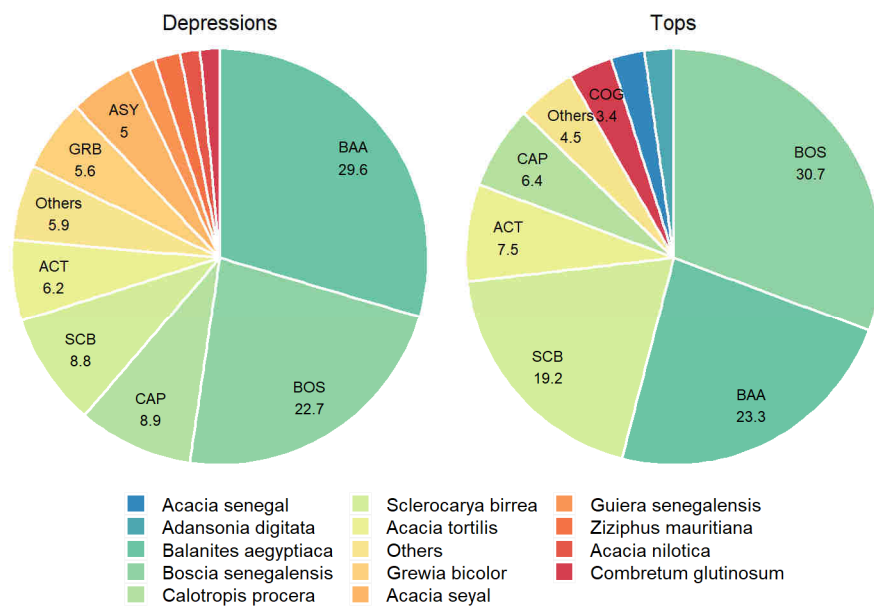


Figure 4.8 – Importance Value Index (%) in depressions and on tops. Species for which the IVI was smaller than 1.5% were gathered under the term “others”.

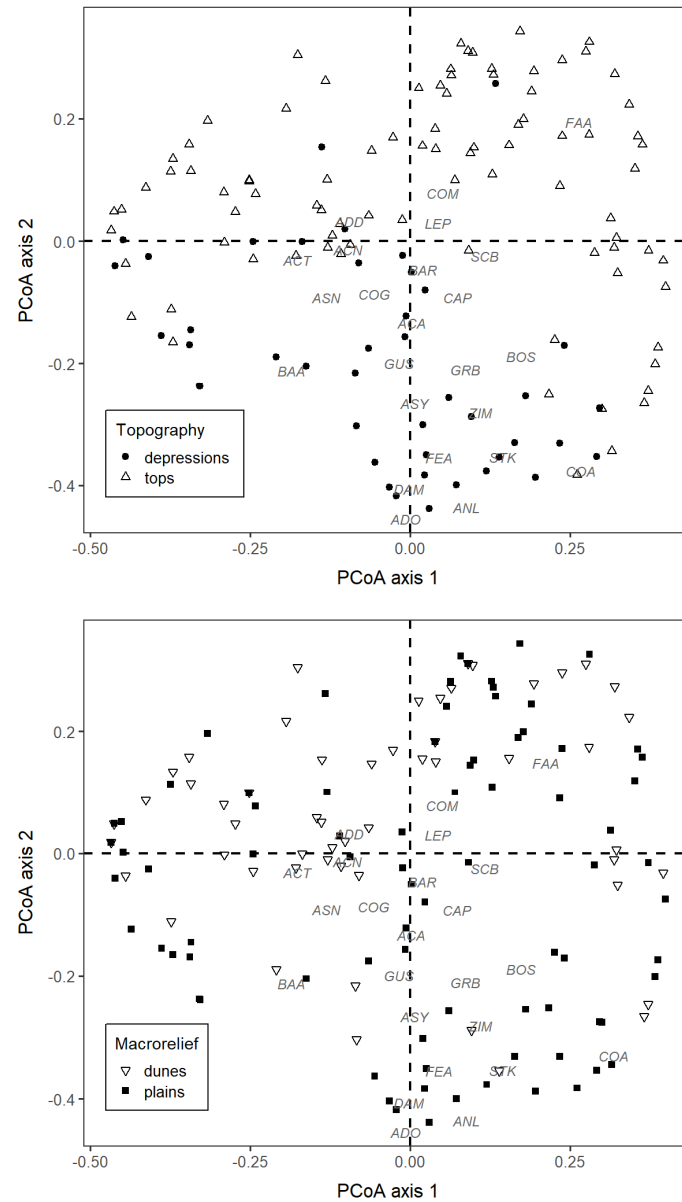


Figure 4.9 – Principal Coordinates Analyses for the adults. Top panel: highlight of the topography. Bottom panel: highlight of the macrorelief.

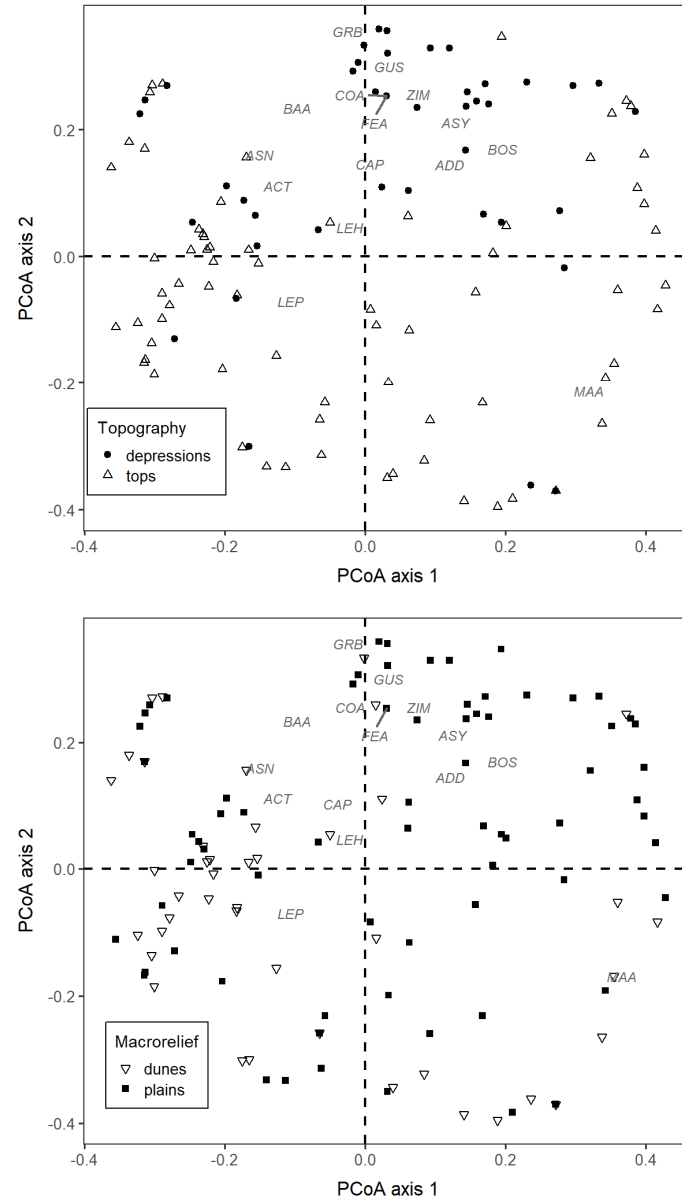


Figure 4.10 – Principal Coordinates Analyses for the saplings. Top panel: highlight of the topography. Bottom panel: highlight of the macrorelief.

Chapter 5

Woody vegetation changes from 1965 to 2018

— *Outline* —

In this chapter, we are dealing with the temporal evolution of woody vegetation since 1965, using field inventory data, satellite images, aerial photos and the Flotrop database. Density and woody cover are analyzed on three types of sites: sites located on dunes, plains, and sites near a Fulani camp that remained at the same location from 1980 to 2018. Specific composition evolution is studied at the scale of the study area. The text is based on the paper of Dendoncker M., Brandt M., Rasmussen K., Taugourdeau S., Fensholt R., Tucker C.J. and Vincke C. *Woody vegetation changes from 1965 to 2018 in the Ferlo (Senegal) using high-resolution imagery and field surveys*, submitted at Regional Environmental Change and accepted with minor revision at the date of July 12 2020. As for Chapter 4, it implies that it can be read as a “standalone” chapter, with some repetitions regarding the state of the art (Chapter 2) and the methodology (Chapter 3).

– *Abstract from REEC* –

Woody vegetation dynamics in the Sahel have been debated since the great droughts of the 1970s-1980s. Here, we combined high-resolution satellite and aerial imagery, field inventory and historical botanical records to study woody vegetation trends over the years 1965, 1980, 2008 and 2018 in the Ferlo, the Sahelian sylvo-pastoral zone of Senegal. While tree density has decreased from 1965 (14.8 trees per ha), to 1980 (13.4) and 2008 (11.9), a stabilization seemingly occurred between 2008 and 2018 (12.2). The relatively moderate decrease in density over 50 years characterized by extensive human pressure and droughts, as well as the rather stable woody cover following the drought years, do not support narratives of widespread desertification in this region. However, we observed a shift in the composition of species. While the drought resistant tree *Balanites aegyptiaca* showed a stable abundance, *Acacia tortilis* showed strong increases and other species like *Sclerocarya birrea* and *Combretum glutinosum* decreased. In addition, the ratio of shrubs vs. trees has increased toward more shrubs in recent field surveys conducted. The observed loss of species diversity combined with the increase of drought resistant species that are sometimes obscured by greening trends, are in line with current observations for savanna ecosystems at a global scale in the context of an increase of aridity.

5.1. Introduction

The vegetation of savanna ecosystems is characterized by the coexistence of woody species and grasses. Savanna is also the typical plant formation encountered in the Sahel, being a semi-arid region in West Africa delimited by isohyets of 200 and 600 mm of annual rainfall. Rainfall in the Sahel is concentrated to a few months during July-September and is characterized by a high spatial and interannual variability (Le Houérou, 1989; Nicholson, 2013). Most livelihoods of the Sahel are concentrated around pastoralism, relying on different strategies to deal with the variable vegetation resources (Thébaud and Batterbury, 2001). In addition to provide fodder to the livestock during the dry season, woody species offer many other ecosystem services such as firewood, fruits or traditional medicine (Lykke *et al.*, 2004; Sop *et al.*, 2012).

During the 1970s and 1980s, concerns were raised about the vegetation in this bioclimatic region, because the Sahel was hit by the most intense drought years of the 20th century with annual rainfall decreasing down to 40% compared to the long term mean (Nicholson, 2001; Nicholson, 2013). Many researches have focused on the impacts of these droughts on vegetation in the region since then (Epule *et al.*, 2014; Gonzalez *et al.*, 2012; Hiernaux *et al.*, 2009). A decrease in density and species richness of woody vegetation was reported in the West African Sahel/Senegal by field inventories, Earth observation datasets or local knowledge (e.g.: Gonzalez, 2001; Gonzalez *et al.*, 2012; Poupon and Bille, 1974; Vincke *et al.*, 2010; Wezel and Lykke, 2006). However, many studies based on remote sensing approaches, have shown that the Sahelian vegetation has experienced a recovery, also called “greening” (interpreted as an increase in gross primary productivity; Sellers, 1985) since the end of the drought years (Anyamba and Tucker, 2005; Dardel *et al.*, 2014; Olsson *et al.*, 2005). These studies have calculated NDVI (Tucker, 1979) from time series of NOAA AVHRR satellite images, allowing yearly estimates of vegetation productivity across the Sahel from 1982 to date. Until recently, it has been difficult to attribute this greening to the herbaceous or/and woody component of the vegetation, but new analyses of both satellite and field data have shown that the major part of the greening could be associates with the woody part (Anchang *et al.*, 2019; Brandt *et al.*, 2019; Brandt *et al.*, 2015).

Still, there are some limitations to these studies due to the focus on the post-drought years and uncertainties remain in our understanding of the long-term vegetation dynamics of the region. First, the greening of the Sahel is not uniform (Brandt *et al.*, 2017; Fensholt *et al.*, 2013) and most satellite data available over a

longer time period have a very coarse spatial resolution making it impossible to study single landscape features like trees. Second, the datasets used generally start in the 1980s, which coincides with the extreme drought period (Mbow *et al.*, 2015). If viewed over a longer period, e.g. from the 1960s to date, only a few robust studies exist (e.g. Brandt *et al.*, 2014; Hänke *et al.*, 2016), due to the absence of relevant and homogeneous data-sources, allowing for a spatially and temporally coherent survey. Third, species and growth forms cannot be identified within satellite images. Moreover, ecosystem services are species dependent (Breman and Kessler, 1995) and if the re-greening is driven by unpalatable woody species, the region's value as pastoral zone is not likely to have recovered. Field inventories thus remain crucial as complementary data sources (Hänke *et al.*, 2016; Herrmann *et al.*, 2005). Unfortunately, there are only few long-term field monitoring sites that allow to study woody species changes (e.g. the experimental trial of Miehe *et al.*, 2010). The observation on these sites included, among others, a decrease in some tree species simultaneously with an increase of bushes and spiny trees (Miehe, 1994; Miehe, 2002).

It is thus currently unclear if the vegetation recovery from the drought (the “greening”) is comparable to pre-drought conditions, or if a real shift in vegetation patterns (change in growth form, density, etc.) and species has occurred. Additionally, local perceptions of land degradation/improvements often disagree with satellite-based analyses, and there is a need for more interdisciplinary studies to bridge the information provided by different methods (Herrmann *et al.*, 2020; Herrmann *et al.*, 2014; Mbow *et al.*, 2015).

This study combines historical and recent satellite images with field data in order to document changes in woody vegetation for an area in the Ferlo (Senegal) between 1965 and 2018. The research includes the use of old de-classified Corona satellite images, which provide useful information about pre-drought conditions (Spiekermann *et al.*, 2015) and historical field data that inform about the species changes. We address three specific objectives: (i) to investigate the changes in woody plant density between 1965 and 2018 and in woody cover between 1980 and 2008; (ii) to determine if the observed changes in woody cover depend on relief and pastoral camps, a proxy for human activities; (iii) to investigate the changes in species composition and in species abundance between 1970 and 2017.

5.2. Material and methods

5.2.1. Study area, indicators and datasets

The study area is part of the Ferlo, located in the Sahelian and sylvo-pastoral zone of Senegal, mainly used by Fulani pastoralists. Human impact is limited to the effects of grazing and browsing, and fuel-wood collection, mainly for local uses. More specifically, the study focuses on an area of approximately 3700 km² (68 km x 55 km), in the surroundings of the deep wells Tessékéré (15.85° N, 15.06° W) and Widou Thiengoly (15.99° N, 15.32° W; Figure 5.1).

The major landform of the Ferlo is composed of fossil aeolian sand dunes intersected by large plains of one to five kilometers (Le Houérou, 1989). Soils are sandy with a slight differentiation according to the landform: ferruginous tropical soils on the dunes and sub-arid red and brown red soils in the plains. Small depressions occur on both plains and dunes but they are more frequent and larger in plains, where they form temporary ponds at the end of the rainy season. This local topography (depressions vs. tops) influences woody vegetation, which preferably grows in depressions where water availability and soil fertility (due to cattle feces and clayey soils) are higher (Dendoncker and Vincke, 2020).

The Ferlo region experienced major changes during the past 50 years. First, permanent water points (deep wells) were installed during the 1950s, providing access to water for population and livestock throughout the year (Le Houérou, 1989). Prior to the 1950s, the region was used only in the rainy season when temporary ponds allowed transhumant pastoralists to enter the region. As ponds dried out during the dry season beginning in November, pastoralists returned to the Senegal River valley or to farming regions in south (Touré, 1990). Second, partly due to the enhanced access to water, both human population and livestock increased. As an example, the density of Fulani camps in a radius of 15 km around the deep well of Tessékéré increased from 0.1 camps.km⁻² in 1980 to 0.23 camps.km⁻² in 2008 (see section 3.2.4). This has raised concerns about the increased pressure of livestock, associated with opening area for year-round use (Le Houérou, 1989). Third, the area suffered from the severe drought years in the 1970s and 1980s, as it was the case for the entire Sahel region. The average rainfall between 1990 and 2007 in the West African Sahel (10° to 15° W) was equivalent to the average of 1970-1989 (Nicholson, 2013), which does not indicate a recovery of the rains to the same degree as for the entire Sahel.

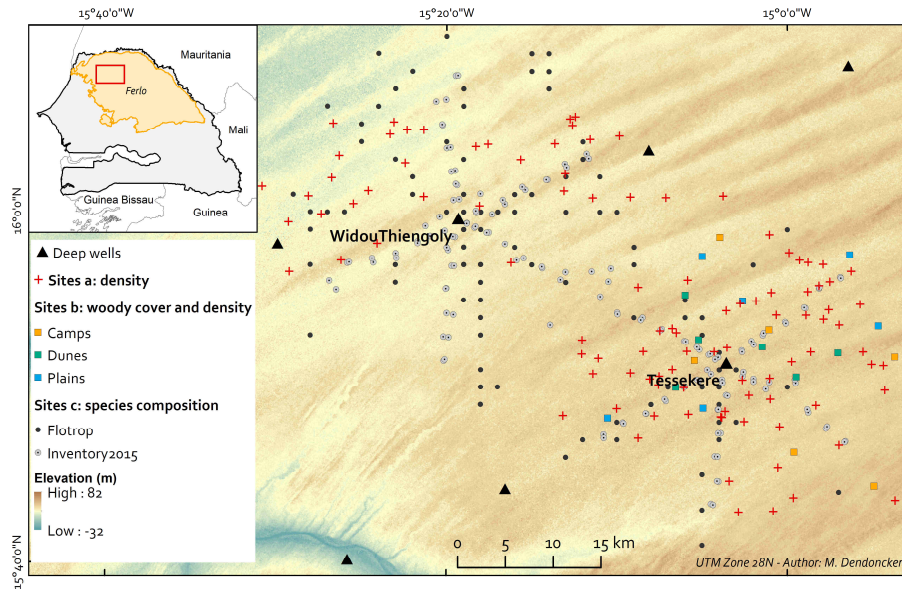


Figure 5.1 – Location of study sites. The three types of sites are shown. The red crosses represent the 100 random plots of 1 ha on which woody plant density was assessed. The squares are the 17 study sites of 1 km² on which woody cover and density were assessed. The circles (grey and black) represent the field plots from the Flotrap database and the field inventory (2015).

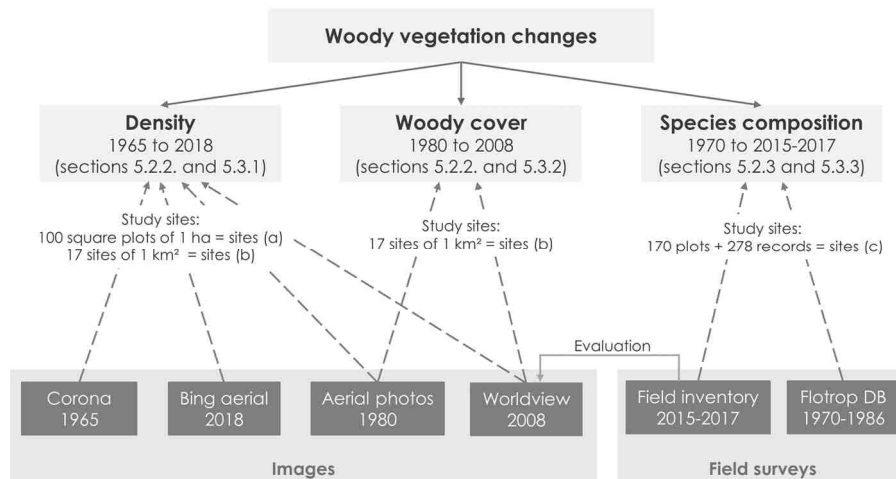


Figure 5.2 – Global methodology to assess woody vegetation changes. Relationships between the three indicators calculated to assess woody vegetation dynamics, the datasets (images and field surveys) and study sites.

This research assesses woody vegetation changes through four indicators obtained from multiple datasets (Figure 5.2). The indicators are: (i) the woody plant density (i.e. the number of individuals per ha); (ii) the woody cover (i.e. the percentage of the ground covered by crowns); (iii) the species composition (i.e. the species list per period); (iv) the frequency of the species (i.e. the percentage of the surveys in which the species are present). The Earth observation datasets (section 5.2.2.1) are used to study woody cover and woody plant density (section 5.2.2.2) whereas recent and historical field inventories enabled us to study the species composition and the species frequency (section 5.2.3).

5.2.2. Woody cover and density changes

5.2.2.1 Earth observations datasets and sampling

Woody cover and plant density were derived from four Earth observation datasets. The first dataset are Corona images available from the U.S. Geological Survey for December 1965 at 2 m resolution. The second dataset are aerial photos taken in January or February 1980, by the Teledyne society for the OMVS (Guissé *et al.*, 1987). The original scale is 1/50 000. The third and fourth datasets are WorldView-1 images from April 2008 (© 2015 DigitalGlobe, Inc. Licensed under NextView) at 0.5 m and Bing map satellite images (© Bing Map Microsoft) from 2018. Even though the spatial resolutions of the data sources are in the same order of magnitude, the different sensors and processing techniques make the detectability of trees and shrubs in the different datasets challenging to compare directly. Figure 5.3 illustrates the differences and shows that only larger trees can be reliably detected in the older datasets (Corona and aerial photos). These differences make an automatic tree detection difficult, and we thus decided for a manual visual interpretation of the images (see section 5.2.2.2).

The Corona and the aerial photos both required georeferencing prior to their use. This was performed using a third order polynomial transformation using large trees as ground control points (at least 40 points per image). The implementation of a systematic geometric correction of the aerial photos was not possible given that the flight information necessary to do such a correction were not available. For that reason, we chose to work only in the central part of the photos (inside a square area of 64 km²) to avoid geometric distortions, which are more pronounced toward the sides.

Two types of sites were sampled. The first type aimed at evaluating the overall trends in woody plant density. Here, we randomly selected 100 plots of 1 ha

within the overlapping areas of Corona images, the aerial photos and WorldView-1 images (sites a, Figure 5.1). The second sampling aimed at testing the influence of human impact (using the presence of pastoral camps as indicator) and relief (i.e. dunes and plains) on woody plant density and cover. We assume that the long-term presence of a pastoral camp induces a higher grazing intensity and woody and non-woody product collection on the surrounding vegetation. We selected 17 sites of 1 km² around the deep well of Tessékéré (sites b, Figure 5.1 and Figure 5.4). Five sites are centered on a Fulani camp present from 1980 (visible on aerial photos) to 2018 (visible on WorldView-1 and Bing images). As Fulani camps are located in plains, no camp sites in dunes could be selected. Additionally, we selected 12 more sites: six on dunes and six in the interdunal plains, all located at a minimum distance of 1 km from camps. To facilitate the reading, we will further refer to the type of site (camp, dune or plain sites) reflecting human activity and the relief.

5.2.2.2 Woody cover and density measurements

Woody plant density reflects the number of woody plants per hectare that are visible in all the imagery used. The detectability of small shrubs and bushes was limited by the data source of poorest quality, being the Corona images. Smaller crowns were thus omitted in all the imagery (Figure 5.3). Density was assessed in the 100 plots of 1 ha (sites a, Figure 5.1) by manually counting the woody individuals visible in the Corona images, the aerial photos, the WorldView-1 and the Bing images. We also performed the same density analysis on the 17 sites of 1 km² (sites b, Figure 5.1) for three image acquisition periods: 1980, 2008 and 2018. We counted woody individuals inside a grid of 100 m x 100 m squares that divided each site into 100 cells.

Woody cover expresses the fraction of the ground covered by the sum of the woody plant crowns vertical projections. This indicator was only calculated for images with a comparable resolution (i.e. aerial photos and WorldView-1 images). Woody cover changes were studied between 1980 and 2008 on the 17 sites of 1 km² (sites b) using the same grid as for the density (the quality of Corona images was not sufficient for this analysis). We used a threshold grey-scale value to classify the pixels into tree versus no-tree. The threshold determination was based on trial and error. Masks were created for the camp sites to exclude the areas occupied by houses and the immediate surroundings of bare soil as their pixel values fell within range of tree pixel values. To validate the thresholds and to be able to estimate a detection error rate, we randomly distributed 100 points

within each of the 17 sites. As woody cover usually ranges from 5 to 10% in our study area (Tappan *et al.*, 2004), we allocated 10 points to the “tree” class and 90 points to the “no tree” class per site. We then visually verified if these points were correctly assigned to the “tree” class or the “no tree” class.

The accuracy of satellite-based woody cover values was evaluated by field data (see Appendix 10 for coordinates). Thirty square plots of 0.25 ha each were inventoried in 2017 in the area around Tessékéré. The field plots were randomly located inside the 1 km² sites (sites b). We recorded every living individual woody plant with a crown diameter larger than 0.5 m ($n = 572$) to match with the resolution of the WorldView-1 sensor. We identified the species and measured two perpendicular crown diameters for each plant. The percentage of overlapping crowns was visually estimated so that the field woody cover would reflect the actual proportion of the ground covered by the vertical projections of the crowns. Field measured woody cover was calculated from the field data of 2017 by summing the crown cover of all individuals corrected for overlapping canopies. For the same 30 plots, woody cover was assessed in the WorldView-1 images by applying the threshold method. A linear regression was then performed between field woody cover and satellite estimated woody cover to evaluate the consistency of the values.

5.2.2.3 Changes from 1980 to 2018 and influence of human impact and relief

To study changes in woody plant density from 1965 to 2018, we compared the density in the 100 square plots (sites a) using multiple Student means comparisons and Holm’s method (Holm, 1979) as p-value adjustment. Due to varying accuracy in georeferencing and distortion of the images, it cannot be guaranteed that the 100 plots perfectly overlay between 1965 and 2018. However, the large number of plots is assumed to be representative for the whole study region so an average over the plots is comparable.

Changes in woody cover between 1980 and 2008 and in density between 1980 and 2018 for the 17 sites of 1 km² were assessed using Linear Mixed Models with Satterthwaite degrees of freedom (Zuur *et al.*, 2009), fitted with the “lmerTest” package in R software (Kuznetsova *et al.*, 2017; R core team, 2018). The response variables were either the density or the woody cover values obtained at the grid scale (i.e. 1700 cells of 1 ha). Site location was used as random effect and we included the type of site as variable with fixed effect (See Appendix 17 for details). For both woody cover and density, the first model aimed to test for

significant changes during the studied period (effect of year) and the general effect of the site type. If the effect of the year was confirmed, we calculated four new variables “delta” to further study the changes and the potential influence of relief and human impact. One delta variable was computed for the woody cover: the cover of 2008 minus the cover of 1980 for each cell and three deltas for the density: density in 2018 minus density in 2008, density in 2008 minus density in 1980 and density in 2018 minus density in 1980. As the datasets from 1980 and 2008 overlaid very precisely, we directly compared the presence or absence of tree between the two dates. This allowed us to obtain, for each site, the proportion of trees that were already present in 1980, which is important for studying age structure of woody plants in the region.

5.2.3. Dynamics in species composition

Field surveys (sites c, Figure 5.1 and Figure 5.2) include records from three different sources. First, the 30 plots that were inventoried (see 5.2.2.2). Second, we used the data from 139 plots inventoried in 2015 in the same area and using a similar field methodology to the inventory of 2017 (Dendoncker and Vincke, 2020). Third, 278 records, dating from 1970 to 1986 and located within an area of 20 km around the deep wells of Widou Thiengoly and Tessékéré, were extracted from the Flotrop database (Taugourdeau *et al.*, 2019). For 143 of these records, the species abundances was recorded using Braun-Blanquet coefficients (Braun-Blanquet, 1932). These coefficients were transformed on relative abundances by dividing each abundance by the sum of the individual abundances. The remaining 135 records contained only information about the presence of species.

The species frequencies in the Flotrop database were compared with the species frequencies in 2015-2017. Species with more than five occurrences in the database (among the 278 records) were classified in three groups: (i) increasing species, i.e. species with a relative difference in frequency $> 30\%$ (arbitrary threshold); (ii) decreasing species, i.e. species with a relative difference in frequency $< -30\%$; and (iii) stable species. For the field survey of 2017, we calculated the density ratio of trees vs. shrubs and bushes. Species considered as shrubs were *Boscia senegalensis* (Pers.) Lam. ex Poir., *Calotropis procera* (Ait.) Ait. f.), *Feretia apodanthera* Del., *Guiera senegalensis* J. F. Gmel., *Leptadenia pyrotechnica* (Forssk.) Decne. Species composition was established for dunes and plains separately.

To study the change of botanical composition between 1970 and 2015-2017, all the abundances of the field surveys were pooled into a matrix with rows as records and columns as the relative species abundances. We then performed a Principal Coordinates Analysis (PCoA) on a Bray-Curtis distance matrix using the “vegan” package in R software (Oksanen *et al.*, 2019). Records were classified in three separate periods: 1970-1971 (corresponding to the early stage of the great drought, $n = 78$), 1972-1986 (during the drought, $n = 65$), and 2015-2017 (the current situation, $n = 169$). The influence of the period on the first two axes of the PCoA was tested by an Anova and Tukey’s test.

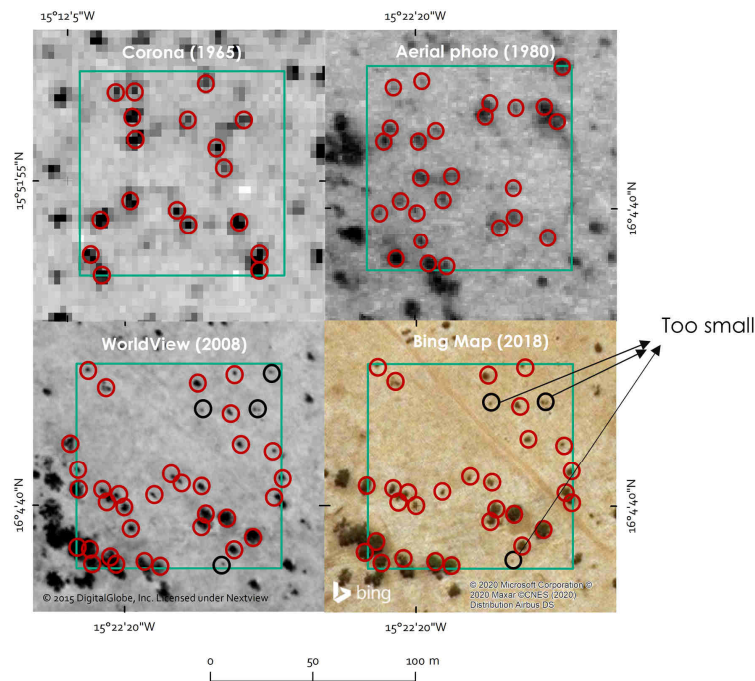


Figure 5.3 – Quality of the four datasets (not the same location except for WorldView and Bing map). The red circles identify woody individuals inside the 1 ha plot in green. The black circles highlight the individuals that were omitted in the WorldView-1 and Bing map imagery because their size was too small to be detectable in the older data sets.

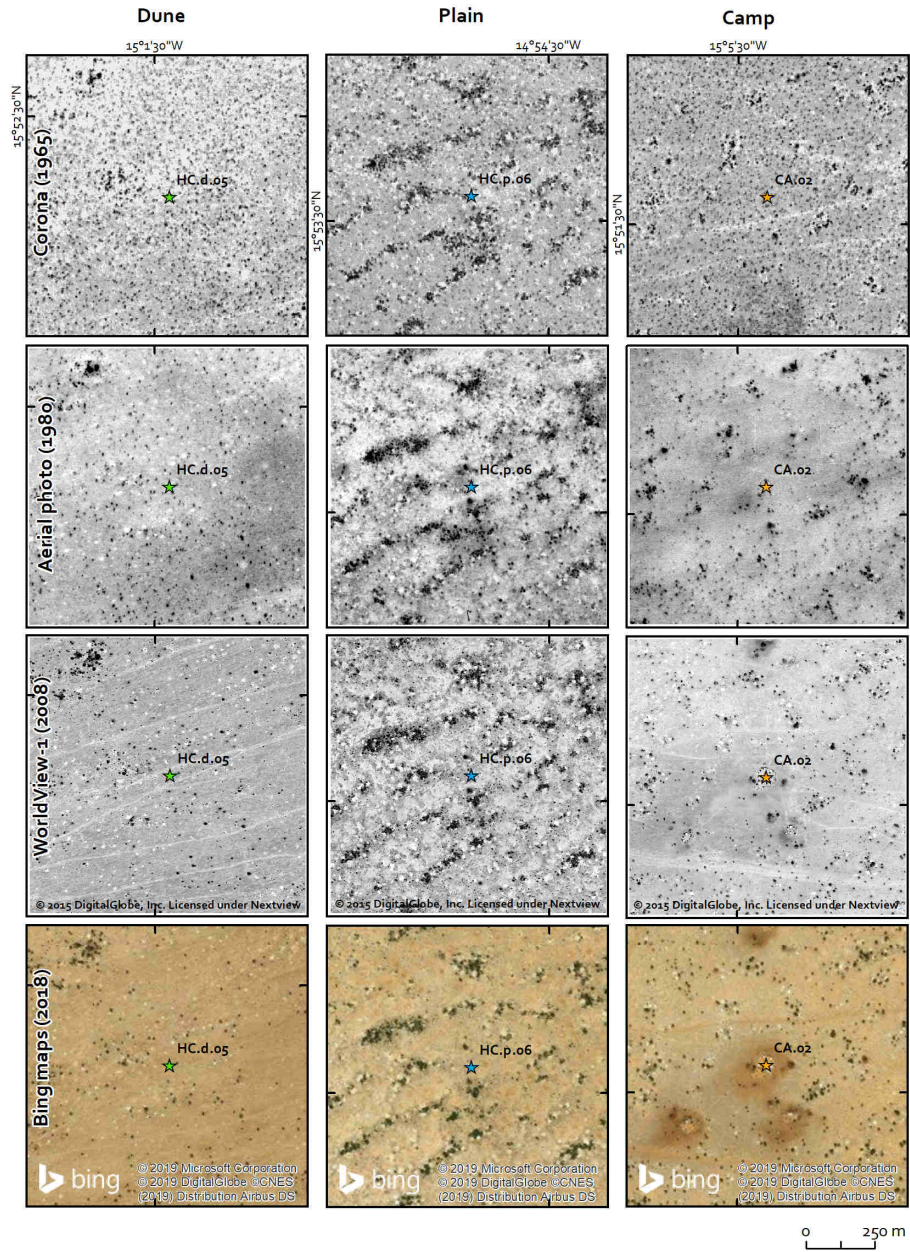


Figure 5.4 – Time series of Earth observations datasets from 1965 to 2018 for each type of site. In rows, the four datasets; in columns, the type of site, with the center marked by a star (a dune site, HC.d.05; a plain site, HC.p.06; and a site near a camp, CA.02).

5.3. Results

5.3.1. Woody plant density

During the period 1965 to 2018, woody plant density decreased from 14.8 ± 5.0 trees.ha⁻¹ ($\pm$ s.d.) in 1965 to 13.4 ± 5.1 trees.ha⁻¹ in 1980 (though not significantly) and reached 11.9 ± 5.7 trees.ha⁻¹ in 2008 in the 100 random plots (sites a, Figure 5.5). No marked differences occurred during the last period with a density of 12.2 ± 5.7 trees.ha⁻¹ recorded in 2018. The pattern was confirmed for the 17 sites (sites b). The first Linear Mixed Model highlighted an effect of the year (Appendix 17), with density values decreasing from an average value (least square means, with a standard error of 0.55) of 14.5 trees.ha⁻¹ in 1980 to 12.3 trees.ha⁻¹ in 2008 but increased to 13.6 trees.ha⁻¹ in 2018 (Figure 5.5). The Tukey test on the least square means differences confirms this trend ($P < 0.001$).

The type of site influences the woody plant density, regardless of the year, as shown by the first model. Plain sites showed the highest woody plant density value with a least square mean of 16.4 trees.ha⁻¹ against 14.5 and 9.5 trees.ha⁻¹ for the camps sites and the dune sites respectively. However, these differences are only significant between plains and dunes, and camps and dunes (Tukey test, $P < 0.05$). Looking at the changes between 1980, 2008 and 2018 according to the type of site, the woody plant density around camps changes from 14, to 13.5, to 15.8 trees.ha⁻¹, respectively. On dunes, woody plant density changes from 11.2 (1980), to 8.2 (2008) to 9.0 (2018) trees.ha⁻¹; and in plains from 18 (1980), to 15.3 (2008) to 16 (2018) trees.ha⁻¹. In relative changes between 1980 and 2008, the most pronounced decrease is observed for dunes (-26.8%) compared to plains (-15%) and camps sites (-3.6%) (Figure 5.5). However, these differences in density changes between the different types of sites are not statistically different according to the three other models (Appendix 17).

5.3.2. Woody cover

5.3.2.1 Evaluation of the WorldView-1 woody cover using field woody cover

The WorldView-1 estimated woody cover from 2008 is highly correlated with the woody cover measured in the field in 2017 (Figure 5.6, $R^2 = 0.807$, slope = 0.89, mean absolute error = 0.63), although the time period is different. Woody cover in depressions is generally overestimated by the satellite assessment, whereas the values are underestimated on dune tops and slopes.

Trees with overlapping crowns in depressions form closed canopy areas. This can lead to the formation of clumps when a threshold is applied (e.g. small areas with closed canopy clustered with each other due to shadows at the edge; Figure 5.4, the “plain” column), and might explain the overestimation of woody cover observed here, in particular in older imagery of lower quality.

The validation (by randomly distributed points) of the threshold-based woody cover estimation showed that in total, 81.2% of the points for the WorldView-1 images and 90.6% for the aerial photos distributed amongst the “tree” class were correctly classified (Appendix 18). As for the “no tree” class, 97.4% of the points for the WorldView and 98.4% for the aerial photos were correctly assigned. To assess whether the observed changes in woody cover are larger than the uncertainty caused by classification errors, we derived a mean error rate of 14.1% from the validation procedure by taking the mean (in %) of the tree points wrongly classified as tree on WorldView-1 and on aerial photos. Changes below this threshold are considered as uncertain.

5.3.2.2 Woody cover changes

The woody cover values for the 17 sites for both image acquisitions are found to be influenced by two factors, as tested by a Linear Mixed Model. The type of site influences woody cover values ($P < 0.001$), independently of the year. Tukey HSD test shows that woody cover values in plains are on average 1.5% higher (least square mean) than the woody cover at camp sites. Woody cover values for dunes sites are in-between and not significantly different from the plains and the camps (Figure 5.4).

Mean woody cover slightly decreased from 1980 (3.9% cover) to 2008 (3.3% cover). The major changes occurred for plains sites, where woody cover decreased from 6.3 to 4.7% whereas for dunes and camps sites woody cover was stable with 2.5 and 2.9%, respectively in 1980, and 2.7 and 2.6% in 2008. However, these temporal changes are not significantly different between the types of site according to the Linear Mixed Model ($P > 0.05$; Appendix 17). The analysis of the presence or absence of tree pixels between 1980 and 2008 (Appendix 19) reveals that for the whole area (represented by the 17 sites), 47.9% of the trees remained unchanged. This means that nearly half of the trees present in 2008 were already visible in 1980.

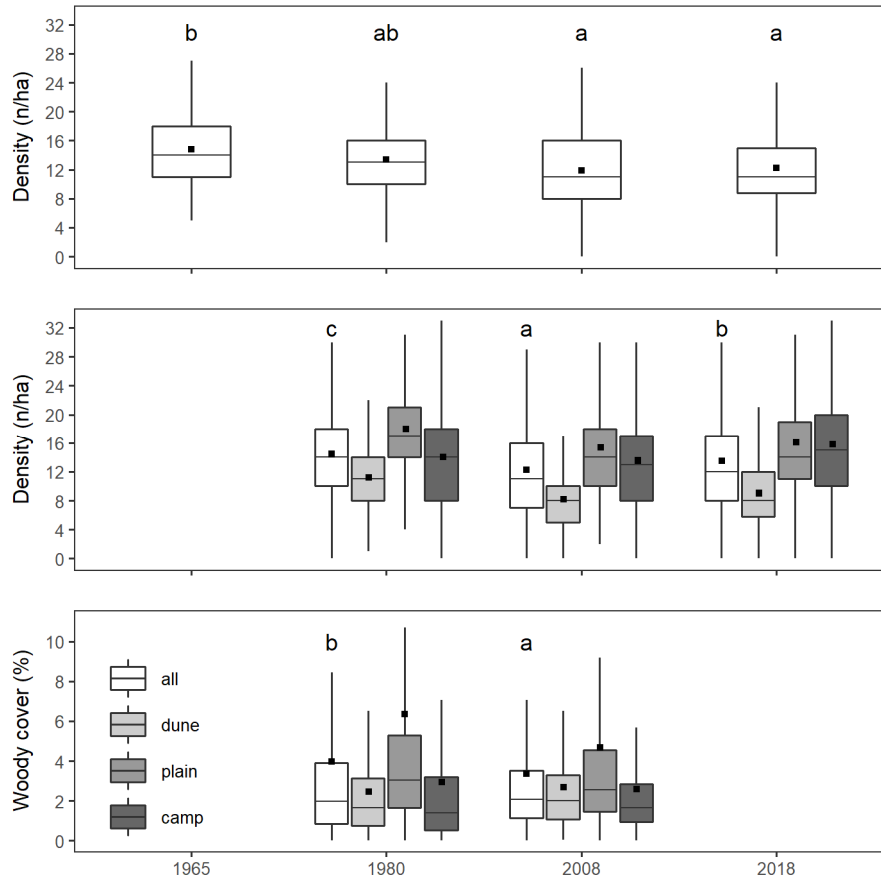


Figure 5.5 – Density and woody cover changes (medians and quartiles) of (from top to bottom): tree density between 1965 and 2018 on the 100 random plots of 1 ha (sites a); tree density on the 17 sites of 1 km² (sites b); and woody cover between 1980 and 2008 on the 17 sites of 1 km² (sites b). Means are represented by the black squares. The letters above the white boxplots indicate whether the values are significantly different ($P < 0.01$) according to Tukey HSD test.

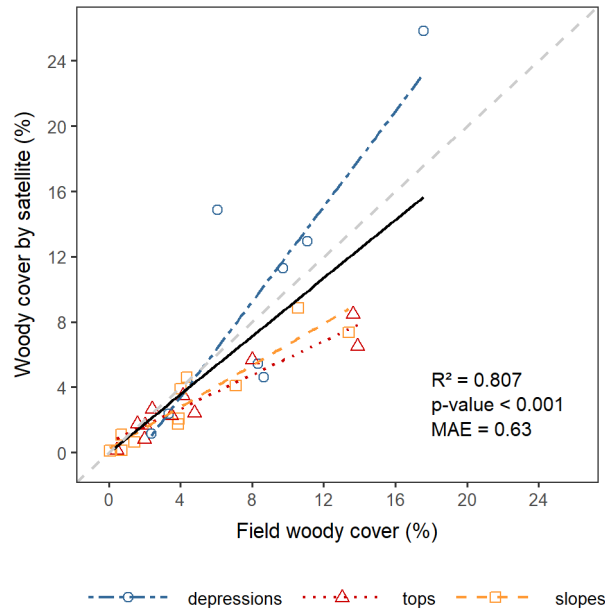


Figure 5.6 – Evaluation of woody cover derived from WorldView-1 with field data ($n = 30$; slope = 0.89). The black line represents the linear regression for all plots, whereas the colored dotted lines separate the plots according to their topography.

5.3.3. Species composition dynamics

We recorded 17 species in the 30 inventoried plots (sites c, see Appendix 20 for the complete list of inventoried species). Amongst these, 15 are found in the plains and 9 on dunes. The most frequent ones are *Boscia senegalensis*, found in 96% of the plots, followed by *Balanites aegyptiaca* (L.) Del. and *Sclerocarya birrea* (A. Rich.) Hochst. both found in 33% of the plots. Less frequent species but still present in more than 10% of the plots are *Acacia senegal* (L.) Willd., *Acacia tortilis* subsp. *raddiana* (Savi) Brenan, *Calotropis procera*, *Combretum glutinosum* Perr. ex DC., *Guiera senegalensis* J. F. Gmel. and *Leptadenia pyrotechnica*. The proportion of shrubs is higher for plains (67%) than for dunes (56%).

The botanical composition has changed from 1970 to 2017. Indeed, the PCoA shows a clear separation between the records of the first two periods (1970-1971 and 1972-1986) and the records from 2015-2017 (Figure 5.7). The Tukey test on the first axis coordinates confirms that trend ($P < 0.001$). This indicates that the communities assemblages (i.e. species that are found together) present in 1970-1971 and in 1972-1986 are not the same as the communities in 2015-2017.

Another finding concerns the currently abundant shrubs species *Boscia senegalensis*, *Calotropis procera* and *Leptadenia pyrotechnica* (field inventories 2015-2017). Both species are located on the right side of the graph, which means that they are more related to the recent field inventories.

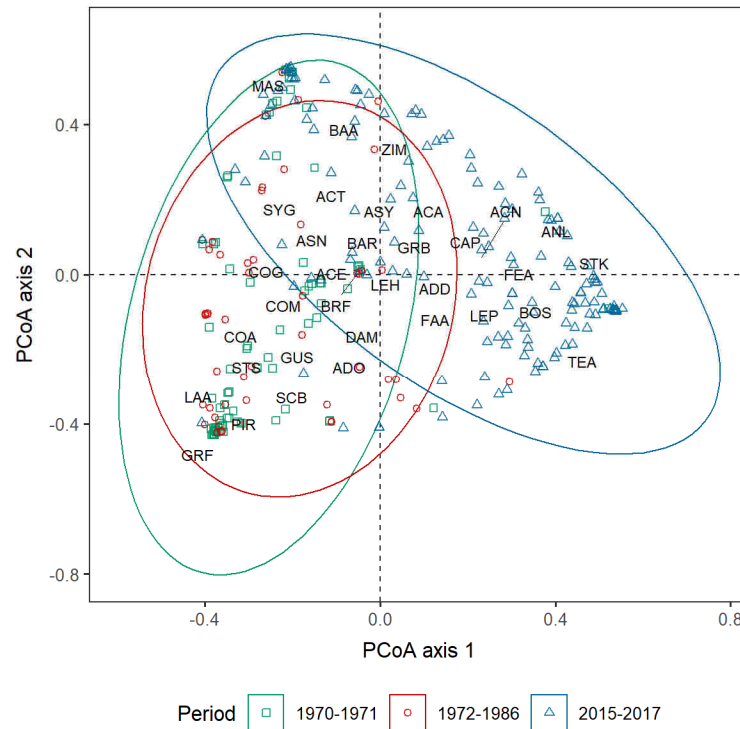


Figure 5.7 – Principal Coordinates Analysis using a Bray-Curtis distance on the abundances matrix of Flotrop and field inventories (2015-2017). Ellipses show the confidence interval at 90% around the records of the three periods. Species are displayed by a three letters acronym: ACA: *Acacia ataxacantha*, ACE: *Acacia erythrocalyx* Brenan, ACN: *Acacia nilotica*, ACT: *Acacia tortilis*, ADD: *Adansonia digitata*, ADO: *Adenium obesum*, ANL: *Anogeissus leiocarpa*, ASN: *Acacia senegal*, ASY: *Acacia seyal*, BAA: *Balanites aegyptiaca*, BAR: *Bauhinia rufescens*, BOS: *Boscia senegalensis*, BRF: *Bridelia ferruginea* Benth., CAP: *Calotropis procera*, COA: *Combretum aculeatum*, COG: *Combretum glutinosum*, COM: *Commiphora africana*, DAM: *Dalbergia melanoxylon*, FAA: *Faidherbia albida*, FEA: *Feretia apodanthera*, GRB: *Grewia bicolor*, GRF: *Grewia flavescens*, GUS: *Guiera senegalensis*, LAA: *Lannea acida* A. Rich., LEH: *Leptadenia hastata*, LEP: *Leptadenia pyrotechnica*, MAA: *Maerua angolensis* DC., MAS: *Maytenus senegalensis* (Lam.) Exell, PIR: *Piliostigma reticulatum* (DC.) Hochst, SCB: *Sclerocarya birrea*, STK: *Stereospermum kunthianum*, STS: *Sterculia setigera*, SYG: *Syzygium guineense* (Willd.) DC., TEA: *Terminalia avicennnioides*, ZIM: *Ziziphus mauritiana*.

Amongst the 40 species recorded in the Flotrop database, half of them only have a few occurrences (< 5) and were therefore excluded from the following classification (See Appendix 20 for the Flotrop species list). The trajectory of six species are classified as “stable”, including *Balanites aegyptiaca* and *Adansonia digitata* L., 13 as “decreasing” and only one (*Acacia tortilis*) as increasing (Figure 5.8). While Figure 5.7 highlighted the disappearance of some communities, this analysis illustrates a strong decrease in relative frequency of many species such as *Grewia bicolor* Juss. (-40%), *Acacia seyal* Del. (-47%), *Sclerocarya birrea* (-48%), *Acacia senegal* (-61%), *Combretum glutinosum* (-70%) and *Commiphora africana* (A. Rich.) Engl. (-96%).

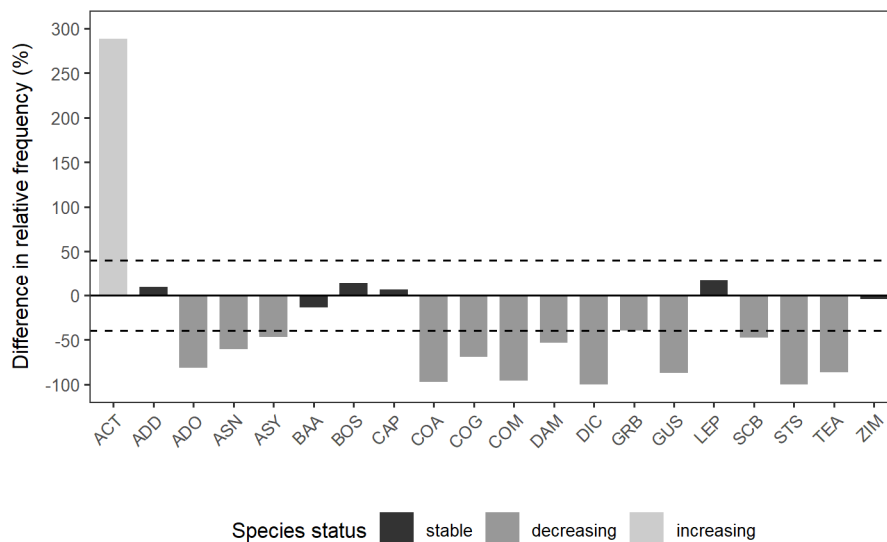


Figure 5.8 – Changes in the relative frequency between 1970 and 2015-2017 for species with more than five occurrences in the Flotrop database. See Figure 5.7 for species acronyms.

5.4. Discussion

Our study shows several patterns regarding changes in woody vegetation in the Sahelian Ferlo over the past 50 years. First, woody plant density was higher in 1965, before the extreme Sahel drought, which was also the case for woody cover in 1980, three years before the driest years of 1983-1984. This is in line with findings by Gonzalez (2001), and confirms that, over the long term, a decline in woody cover has taken place. However, a reduction from 14.8 trees.ha⁻¹ to

11.9 trees.ha⁻¹ over 50 years of extensive human expansion is not a dramatic figure. Besides, the exact size of the change is difficult to establish, given the big differences in spatial resolution of the data.

Second, only minor changes in woody cover not exceeding the classification uncertainty were observed over the past four decades. The relatively stable woody cover does on the one hand refute narratives about widespread desertification after the drought years exaggerated by increased livestock pressure. On the other hand, some studies reporting an increased woody cover at a larger scale (Anchang *et al.*, 2019; Brandt *et al.*, 2019) seem not to be supported at the study area scale. However, here one has to note that other studies start during or after the drought years, while our images were taken a few years before the driest years of 1983-84. It is thus possible that a reduction in tree cover has taken place after 1984, which has been slowly recovering in the following decades.

This is supported by the increasing trends of density found between 2008 and 2018. Similar patterns (decrease in density and/or woody cover followed by a stabilization or an increase) have been observed on sandy soils using field data from Mali (Hiernaux *et al.*, 2009), as drought (1984) induced woody plant mortality was followed by recruitment, though with different timing and magnitude according to the sites. Zwarts *et al.* (2018) also noted a decline in woody cover from 1965 to 2016 in south Mauritania and northern Senegal, but with no changes from 1965 to 1972 and a small increase from 2003 to 2016 (4.1 to 4.9%), suggesting that the decrease happened during the 1973-2002 period. The relief and the presence of camps impact the initial values of woody cover and density, with a higher density and cover in plains. The major decrease occurred in plains, though the difference with the dunes was not significant. Lykke *et al.* (1999) observed a similar phenomenon in Burkina Faso between 1955 and 1995, with the steepest decline of woody cover and density in valleys systems.

Third, we find a shift in the botanical composition toward more *Acacia tortilis* at the detriment of all other species. This supports a study by Brandt *et al.* (2014), which was based on interviews with the local population in Senegal. An increase of *Acacia tortilis* was also reported by interviewees from Burkina Faso who also perceived a decline of all other species (Lykke *et al.*, 1999). Furthermore, species like *Sclerocarya birrea* are reported to be decreasing (Dendoncker and Vincke, 2020; Miehe, 2002) though it was once considered as a dominant component of the woody vegetation for the center of the Ferlo, as mentioned in the vegetation classification of Tappan (1986). We also showed that shrubs species (*Boscia*

senegalensis, *Calotropis procera* and *Leptadenia pyrotechnica*) are more present in the recent inventories. This may indicate a shift in the growth form that took place during the “drought recovery”. Our findings are supported by studies from Widou Thiengoly showing a decline of *Sclerocarya birrea*, *Combretum glutinosum* and *Acacia senegal* and an increase of *Acacia tortilis* and *Boscia senegalensis* (Miehe, 2002). As bushes provide different ecosystem services as compared to trees (e.g. carbon stocks, soil organic matter, fruits, fodder, etc.), this shift is important to consider, in particular in the understanding of the regreening Sahel. If the greening is related with a shift toward more shrubs and less trees, the positive effects may be questioned. Distinguishing shrubs/bushes from trees is difficult using satellite and aerial images, and the uses of field survey and historical records turned out to be critical in for this result.

Gonzalez *et al.* (2012) stated that the dominant factors of the observed vegetation changes are climatic, while acknowledging an influence of human activity on density and species richness at a more local scale. Experiments with study plots being fenced and not grazed over several decades confirmed that grazing induces a shift and a reduction in species diversity with grazing intensity (Miehe, 2002). Yet, no evidence of a negative impact of livestock on woody or herbaceous vegetation cover was found by Rasmussen *et al.* (2018). On the contrary, one aspect of livestock impact is that it concentrates nutrients through dung decomposition around human settlements, which induces a higher productivity.

According to the mixed models, there is no significant differences in woody cover and density changes between the surroundings of camps sites and dunes or plains, supporting Rasmussen *et al.* (2018). Separating the causes (climatic or anthropogenic) of vegetation changes was beyond our objectives, but our results give no evidence that pastoral settlements impact on woody plant dynamics, at least not locally. Yet, we did not study the influence of camps on species composition.

The comparison of different panchromatic images from varying sensors covering five decades is challenging. Given these difficulties, the numbers reported here should be interpreted with caution. The image quality of current satellite systems is far superior to historic aerial and Corona photography. In particular, the Corona cameras were installed on satellites to gather information in times of the cold war, but never had the purpose of being accurate and being used for scientific purposes. Still these systems are a very rare image source from the very wet 1960s and provide valuable information on the times before the great drought.

Our numbers and also the trends are largely in line with Gonzalez (2001) who used aerial images from 1954, giving confidence in our results. We have chosen a visual approach based on the number of trees, as well as a digital classification approach based on the greyscale values. Both approaches include uncertainties. The manual counting as well as the choice of the threshold are subjective; however, a careful validation (field evaluation and classification validation) gives an estimation of the uncertainty of the approach. Moreover, the combination of a manual and automatic approach pointing both in the same direction shows that the results can be considered as robust.

5.5. Conclusion

This research offers insight on long-term changes in woody vegetation (1965-2018) in the Senegalese Sahel using several indicators (density, woody cover, species composition and species frequencies). They were derived from field records combined with satellite imagery, to acquire complementary indicators on ecosystem dynamics. Indeed, geotagged field data combined with a database such as Flotrop and historic Earth observations datasets (Corona images, aerial photos) proved to be very relevant for this topic. We therefore encourage future studies to further combine inter-disciplinary topics using field and satellite data (Herrmann *et al.*, 2020; Herrmann *et al.*, 2014; Mbow *et al.*, 2015). Our results document a reduction in woody plant density from before to after the great drought (1970s-1980s), with a slight recovery in recent years. While the decreasing trends of woody vegetation density and cover observed from 1965 to 2008 has stopped during the last decade (2008-2018), current communities are of different types than before the drought in terms of species composition and growth form. Indeed, the current trees-shrubs ratio tends towards more shrubs. Among the trees, we may be witnessing a shift towards drought resistant species (*Acacia tortilis*) with a better ability to regenerate (*Balanites aegyptiaca*). Our results reflect the current trends reported at a global scale for savanna biomes with drought-induced vegetation diebacks, a more arid climate in drylands and losses in biodiversity towards drought resistant shrub species (Berdugo *et al.*, 2020; Sankaran, 2019). These changes in structure and composition of savanna vegetation are susceptible to bring major modification on ecosystem functioning and ecosystem services provided by savanna biomes (Osborne *et al.*, 2018; Sankaran, 2019).

Chapter 6

A trait-based approach of woody vegetation

— *Outline* —

This chapter mobilizes data from field inventories, Flotrop database, remote sensing, and literature on species traits. We are dealing with the question of the ecosystem capacity to respond to disturbances and to persist through time while providing ecosystem services. Functional diversity concept is used to study the woody vegetation potential response to three main disturbances (grazing, drought and fire) and its effect on two functions (primary productivity and biogeochemical cycles), which support several sets of ecosystem services (provisioning and regulating). First, we investigate the changes in functional diversity (FRic, CWM, functional redundancy and response diversity) and pool of traits from 1970 to 2015, considering three periods (before, during and after the great drought). Indeed, we outlined a decrease in specific richness in Chapter 5 and we seek to know if these changes are reflecting themselves at a functional level. Second, as topography is a major driver of several vegetation characteristics, such as species richness and density, we focus on the influence of topography on the current functional diversity of woody communities.

6.1. Introduction: functional diversity and ecosystem functioning

Woody vegetation provides many ecosystem services to the local population within the study area (see section 2.2.3). However, at this point, it remains unclear how the vegetation influences the ecosystem processes that underlie such services. In addition, the capacity of woody vegetation to persist in the future, and therefore to continue to offer ES, is unknown. To forecast this ability, it is crucial to understand how the vegetation responds to disturbances.

Functional diversity (FD) has previously been defined as a key biodiversity component to understand how the organisms affect the ecosystem functioning and how they respond to environmental pressures (see section 2.4 for the definitions of FD, effect and response traits). In this chapter, we will therefore focus on the species pool present within the study area and therefore, the pool of functional traits.

Indeed, it has been largely suggested that a trait-based approach explains the ecosystem functioning, as functional diversity is by definition tightly related to the ecosystem processes. Harrison *et al.* (2014) precise that functional diversity “is one of the most important biodiversity attributes affecting ecosystem services by impacting the underlying ecosystem processes”. Besides, several studies have used FD components to predict ecosystem functioning (Flynn *et al.*, 2011; Gross *et al.*, 2017; Le Bagousse-Pinguet *et al.*, 2019) or as a resilience indicator (Chillo *et al.*, 2011; Mori *et al.*, 2013; Mouillot *et al.*, 2011; Sterk *et al.*, 2013).

Interactions between functional traits and ecosystem can be apprehended in two ways. Species that have a similar effect on a particular ecosystem function can be gathered into “functional effect groups” (e.g. the N-fixers). The same goes for species that have a similar response to a particular disturbance, they can form “functional response groups” (e.g. the drought avoiders; Figure 6.1). We are aware that the creation of functional groups might not be an ideal approach because of the loss of information that can result from such a clustering (Villéger *et al.*, 2008). However, we use this concept to simplify the understanding of the approach and facilitate the explanation of the links between species composition and ecosystem functioning.

One practical consequence of having a high functional diversity is that the loss of a species will likely not cause the loss of some effect on ecosystem functions. For instance, if we have more than one species that have the same effect on

ecosystem (e.g. three N-fixing species), the loss of one of these species will not have an impact on the N-fixing process in the ecosystem since the other species could replace the first. The “number of species contributing in a similar way to an ecosystem function” is called the functional redundancy (Figure 6.1; Laliberté *et al.*, 2010). Functional redundancy can thus play a role in supporting ecosystem functioning in case of species loss (Naeem, 1998).

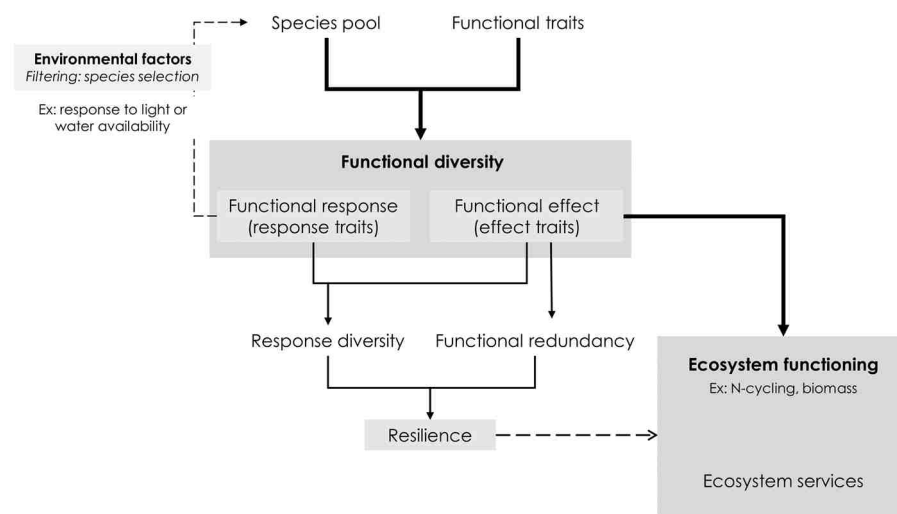


Figure 6.1 – Relationships between functional diversity and ecosystem functioning through the effect and response components of FD. Functional diversity, through the effect component, underlies the ecosystem functions, which support the ecosystem services. Environmental factors will interact with the response strategy of species to filter the species that will persist in the ecosystem. This mechanism will thus determine the species pool. Response diversity and functional redundancy can enhance the resilience of the ecosystem, ensuring its long-term functioning.

However, if the three N-fixing species react the same to a disturbance (for instance, they could all be sensitive to drought), they might all decrease or even disappear consequently to a drought event. In that situation, the nitrogen cycle of the ecosystem will be affected. To maintain the desired tree effects on ecosystem functions, it would have required a different response pattern between these three species (e.g. a more drought-resistant species among the three N-fixers). Response diversity (Figure 6.1) is defined as the “range of reactions to environmental change among species contributing to the same ecosystem function” (Elmqvist *et al.*, 2003); or “the diversity of species that can perform

similar ecosystem functions but have different capacities to respond to disturbance, imparting greater resilience to the entire system” (Mori *et al.*, 2013). While a high functional redundancy does not necessarily guarantee a high response diversity (Mori *et al.*, 2013), a reduction in the response diversity is likely to induce a decrease in the system resilience.

This chapter undertakes a trait-based approach to test two hypotheses. The first one is that the changes in specific composition at the *regional* and *community* scale from 1970 to 2015-2017 (Chapter 5) have respectively impacted the pool of species traits present within the study area (regional scale) and the FD indices (community scale). The second one is that topography influences functional diversity of woody communities as this factor (proxy for water availability) plays a major role in the vegetation differentiation (density, woody cover, species composition and richness; see Chapter 4). A community is an assemblage of species living and interacting in the same location, so in our case that would correspond to an inventory plot of 0.25 ha or a botanical record in the Flotrop database.

The temporal changes of the species pool and FD indices (hypothesis 1) allow to study the species response strategies to three disturbances (via three sets of response traits). We also look at the consequences of these changes on ecosystem functioning via two sets of effects traits related to two ecosystem functions: primary productivity and biogeochemical cycles. The analyses are conducted at two spatial scales. First, we study the functional pool of traits present *within the study area* (regional scale) before and after the great drought. For the response to disturbances, we investigate to what extent the species only present before the great drought exhibit different response strategies (i.e. traits values combinations) from the species still present today. For the effect traits, we compare the combinations of effect traits, which express ecosystem functionalities, of the current vegetation to the effect traits combinations of the vegetation before the great drought. Second, the changes in functional diversity, both response and effect, at the community scale, from before to after the great drought (the three periods described in section 3.2.3.2) are being evaluated via two indices: FRic and CWM.

For the second hypothesis, we assess the current functional diversity of woody communities on tops vs in depressions, through five FD indices (FRic, FEve, FDiv, FDis, CWM), on the same three sets of response traits and the two sets of effect traits used in the temporal changes evaluation.

6.2. Methodology

6.2.1. The response-effect trait-based approach: overview

A trait-based approach can be decomposed in four steps (Figure 6.2). First, species concerned by the approach have to be listed. Here, we are interested in species encountered during the inventories of 2015 and the species recorded in the Flotrop database (Taugourdeau *et al.*, 2019). Second, traits data have to be searched and gathered (see section 3.3.4). Third, traits are grouped in “response sets” and “effect sets”. The “response sets” gather the traits that influence the plant response to pressures via their impact on species growth, reproduction and survival, and subsequently the plant fitness, which will determine its persistence (Violle *et al.*, 2007). The “effect sets” are constituted of traits that affect ecosystem process. These three first steps have been explained in Chapter 3, section 3.3.4.

Steps	Details	Sections
(i) Listing the species considered	Species encountered in 2015-2017 (field inventory) and recorded in Flotrop database (1970-1986).	3.3.4
(ii) Gathering the data on traits	From literature review and expert knowledge.	3.3.4
(iii) Response and effect traits	Grouping traits in sets according to their links with the targeted pressures (response traits) and functions (effect traits).	6.2.2
(iv) Analyses: two temporal scales	Functional space, FD indices	6.2.3
	↓	6.2.4
	1. Changes from 1970 to 2015 Pool of traits, FD indices, response diversity	6.2.5
	2. 2015 FD indices, response diversity	6.2.6

Figure 6.2 – Responses and effects trait-based approach: overview of the four steps and corresponding sections.

The studied disturbances, functions and the sets of traits are described in section 6.2.2. The final step is the analysis of these sets, according to our objectives. The analyses are carried out at two temporal scales (from 1970 to 2015 and in 2015),

each corresponding to one of our hypotheses stated in the introduction (6.1) and are detailed in section 6.2.4, after having explained the computation of FD indices in section 6.2.3.

6.2.2. Response and effect traits

6.2.2.1 Studied disturbances and functions

We are interested in three environmental key disturbances that potentially influence woody vegetation in our study area: grazing by livestock, drought and bush fire, for which we give the definitions adopted in this work and the reasons to study it. First, grazing by livestock includes all the removal of woody plant parts (leaves, twigs, bark, or sometimes the whole plant when it comes to the seedlings) by grazers and browsers. This pressure is currently intense given the pastoralism land use. It can affect the woody vegetation either by damaging adult trees but it especially has an effect on the regeneration, as seedlings and saplings are more vulnerable given their small height.

Second, droughts considered here are extreme events, which means that they exceed the adjustment of present species and can therefore induce dieback and/or mortality. We do not consider the annual water deficits brought by the succession of seasons. We make no differences whether the drought is due to climate change or not and whether it lasts one year or more. Sahelian countries have experienced several droughts episodes during the 20th century and with climate change, extreme events are expected to increase in frequency. Besides, the IPCC projects that the stress of water availability in Africa will be exacerbated by climate change (IPCC, 2014a).

Third, fire is one of the main determinants of woody cover in savannas (Sankaran *et al.*, 2005). It can cause partial or complete destruction of woody plants. We include both accidental and human induced fires. Fire mostly induces mortality on the seedlings, saplings and young plants. Although the occurrence of fires is low in the north of the Ferlo, they became more frequent in the south (Bremen and Kessler, 1995). Bille *et al.* (1972) estimated the fire frequency at one every five years during the early years of the great drought. In the context of increasing aridity, fires might become more frequent (Siyum, 2020). However, fires within the study area are more intense during the years with high rainfall when there is enough (herbaceous) biomass to propagate it. Le Houérou (1989) stated “because of range depletion and reduction of biomass, fires are not as destructive

as they used to be”. Therefore, this pressure does not present a clear increasing or decreasing trend.

We are aware that these disturbances can have negative and positive impacts. For instance, moderate grazing can favor some species (Miehe, 1994; Miehe, 2002). It should also be noted that interactions exist between the studied disturbances. For instance, following the great drought, the number of animals considerably decreased, which created a temporary reduction of the grazing pressure. However, we do not take into account these kind of feedbacks in our analysis. If a relation between a given trait and a disturbance is recognized in the literature, we include this trait in our analysis, without applying an “intensity threshold” to the relation and without knowing the strength nor the direction of the relationship between disturbances and vegetation response.

In addition, the effect of woody vegetation on two key ecosystem functions, primary productivity and biogeochemical cycles, are studied through effects traits. The primary productivity function underpins provisioning ecosystem services such as wood or fodder production. It is also linked to the regulating service of carbon sequestration, through the production of wood and litter. The biogeochemical cycles function (decomposition, mineralization and mobilization of elements) underlies some key regulating services such as soil fertility (MEA, 2005). These two functions are generally the ones that are studied in research dealing with functional diversity and ecosystem functioning (e.g. Gross *et al.*, 2017; Laliberté *et al.*, 2010; Lavorel and Garnier, 2002). Besides, these two functions are likely to be affected by the increasing aridity in drylands due to climate change (Berdugo *et al.*, 2020). Following the same logic as for the functional response, we do not know the exact effects that result from the trait combinations; the direction and the intensity of the links (i.e. the ecosystem processes) are not explicit.

6.2.2.2 Sets of response and effects traits

Traits (both response and/or effect) can be classified in different groups according to what part of the plant they describe or what function they express (Table 6.1). We retained the five classes of Pérez-Harguindeguy *et al.* (2013): whole plant traits, leaf traits, stem traits, belowground traits and regenerative traits. All the traits have been described in section 3.3.4. Despite the intra-specific variability of traits, we assume that the inter-specific variability is higher, thus maintaining the functional classification of species.

Table 6.1 – List of the traits integrated in the functional diversity analyses. The last column indicates in percent for how many species the trait values were found. Traits are listed alphabetically within each category. Note: table identical to Table 3.5.

Traits	Type	Units or attributes	Completeness (%)
Whole-plant traits			
Growth form (form)	categorical	tree, bush, shrub	100
Maximum height (h.max)	continuous	m	100
Spinescence (spin)	ordinal	from 1 (no spine) to 4 (numerous, hard, long spines)	100
Leaf traits			
Digestible protein (pr.dig)	continuous	% of dry matter	74
Leaf area (lf.are)	continuous	mm ²	59
Leaf area category (lf.siz)	categorical	nanophyllous (20–200 mm ²), microphyllous (2–6 cm ²), submicrophyllous (6–20 cm ²), mesophyllous (20–100 cm ²).	72
Leaf N content (lf.N)	continuous	mg.g ⁻¹	90
Leaf P content (lf.P)	continuous	mg.g ⁻¹	82
Leaf persistence (lf.per)	categorical	deciduous, evergreen, semi-evergreen	100
Leaf phenology (duration of leafing period) (lf.mth)	continuous	months	87
Specific leaf area (SLA)	continuous	mm ² .mg ⁻¹	41
Stem traits			
Bark thickness (bk.th)	ordinal	from 1 (thin) to 3 (thick)	100
Stem specific density (wood density) (wd.den)	continuous	g.cm ⁻³	92
Vessel area (vs.are)	continuous	mm ²	59
Below-ground traits			
N fixer (N.fix)	categorical	yes or no	87
Presence of a taproot (taprt)	categorical	yes or no	46
Regenerative traits			
Dispersal mode (disp)	categorical	anemochorous, zoochorous	97
Fruit length (fr.lg)	continuous	mm	90
Resprouting capacity (coppice) (cop)	categorical	yes or no	87
Root suckering capacity (rt.suc)	categorical	yes or no	72
Seed weight (sd.w)	continuous	mg	97

Table 6.2 – Response and effect traits linked to the disturbances and ecological functions. See Appendix 13 for literature sources linking the traits to the disturbances and functions. Traits are listed by alphabetical order.

Disturbance	Response traits
Grazing	digestible proteins
	dispersal mode
	leaf area
	leaf phenology (duration of leafing period)
	maximum height
	resprouting capacity
	spinescence
Fire	bark thickness
	dispersal mode
	leaf phenology (duration of leafing period)
	maximum height
	resprouting capacity
	seed weight
	specific leaf area
Drought	bark thickness
	growth form
	leaf area
	leaf persistence
	leaf phenology (duration of leafing period)
	root sucker
	resprouting capacity
	specific leaf area
	seed weight
	taproot
	vessel area
	wood density
Ecosystem function	Effect traits
Primary productivity	growth form
	leaf area
	leaf N content
	maximum height
	specific leaf area
	wood density
Biogeochemical cycles	growth form
	leaf area
	leaf persistence
	leaf phenology (duration of leafing period)
	leaf N and P content
	maximum height
	N fixer
	resprouting capacity
	specific leaf area
	wood density

Five sets of traits have been created, one for each pressure and one for each function studied. Table 6.2 presents the traits for each of these sets. Following the literature review (see section 3.3.4), some traits, initially linked to the studied disturbances or functions have been discarded from our trait-based approach due to a lack of information for them and are not presented here. We usually kept the traits for which we managed to have the attributes for at least 60% of the species list (i.e. for 23 species over 39). An exception was made for the SLA (41% of completeness, Table 6.1) and the presence of a taproot (46% of completeness). We kept the SLA, as it is a key trait, mentioned in many studies dealing with FD and ecosystem functioning (Diaz et al., 2004), and the presence of a taproot was the only trait giving information about rooting depth.

6.2.3. Assessing functional diversity: computing FD indices

The assessment of the functional diversity of a community implies positioning the species within a functional space. To do so, the relationships between species and more specifically, the functional dissimilarities (i.e. how different the species are, in terms of functional traits) are calculated in order to obtain a matrix that gives the dissimilarity between all the pairs of species. The distance metric used depends on the type of traits. If all the traits are continuous, Euclidean distance can be applied. As we are dealing with several types of traits (continuous, categorical and binary) and missing values in some cases, we had to use Gower's distance (Gower, 1971, see Appendix 3 for dissimilarities measures). The functional space is then build using a specific framework: either a functional dendrogram (1D) or a multidimensional functional space. Finally, the FD indices (see section 2.4.2) are computed based on this functional space.

Two types of data, arranged into matrices, are required (Figure 6.3). First, the abundance matrix (or presence-absence matrix if the species abundances are unknown) regroups, for each community (in rows), the species abundances (in columns). Second, the functional matrix gives for each species (in rows) present in the regional pool (i.e. inside the study area), its attributes for the studied traits (in columns).

As explained in the previous section (6.2.2.2), traits values were not available for all the species, which means that the functional matrix contains missing values. For the continuous traits, we first attempted to fill the gaps using the dissimilarity function provided by Taugourdeau *et al.* (2014). This function used the principle

that species with the same functional strategy present similar traits values (Diaz *et al.*, 2004; Westoby *et al.*, 2002). To replace the trait value t for a particular species s , it selects the species presenting a high similarity degree with the species s , based on the other functional traits, and calculates the median value of the trait t to fill the missing value (see Appendix 22 for details). Despite the use of this function, a few missing values can remain among the continuous traits in case the species with values to be replaced is functionally unique or if the functionally close species also present missing values.

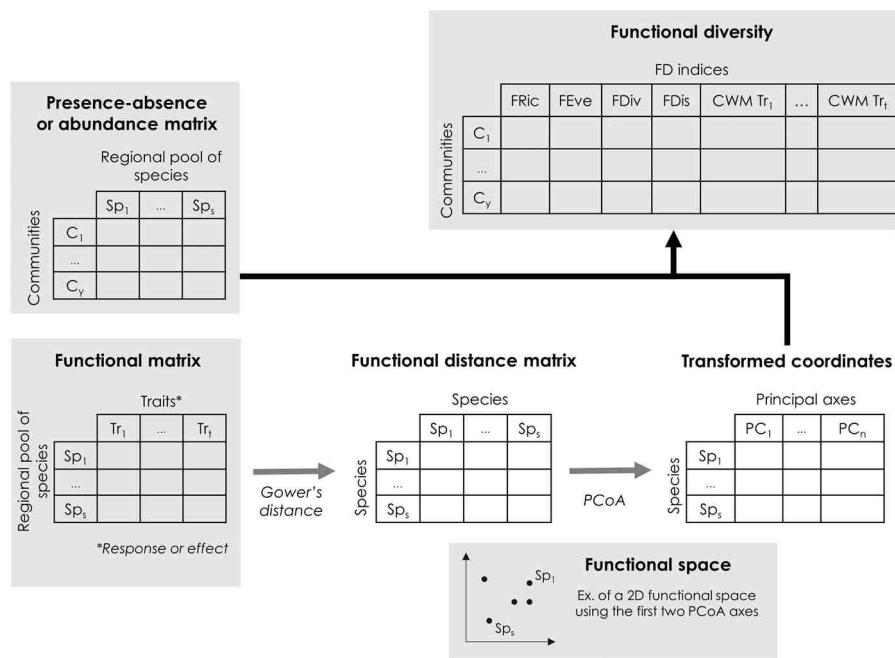


Figure 6.3 – Framework for computing FD indices for communities. Two matrices are required: (i) the presence-absence or abundance matrix, which provides the abundances of species for each community (e.g. an inventory plot, from 1 to y) and (ii) the functional matrix, which gathers the (response or effect) traits values (attributes, from 1 to t) for all the species (from 1 to s) of the regional pool. The distance between all pairs of species is computed using Gower's distance. A PCoA is then used to build the functional space. FD indices are calculated for each community using the principal axes (from 1 to n) coordinates of the species and the abundance matrix.

Gower's dissimilarity (Gower, 1971) is then applied on the functional matrix in order to obtain the functional distance between all pairs of species gathered in the functional distance matrix. The functional space is provided by implementing a Principal Coordinates Analysis (PCoA) on the functional distance matrix. The number of axes of the PCoA ranges from two to the number of species minus one.

The different FD indices are then computed by taking a subset of the axes of this PCoA as “new traits” instead of using all the traits. This reduction of functional space dimensions permitted to deal with situations where there is less species than traits, which is not handled by the FRic and FDiv indices of Villéger *et al.* (2008). PCoA is also convenient when we have a large number of traits, which could make the computation of FD indices more laborious if functional space were directly build from them (Legras *et al.*, 2019). PCoA also produces independent axes, thus allows to deal with the collinearity of the traits (Legras *et al.*, 2019).

We used the FD package in R software (Laliberté *et al.*, 2014), which provides the *dbFD* function for the calculation of functional diversity indices. This function completes the steps of building the functional space and returns, among others, the following indices: the three FD indices of Villéger *et al.* (2008), i.e. the functional richness (FRic), the functional evenness (FEve), the functional divergence (FDiv); the functional dispersion (FDis, Laliberté and Legendre, 2010); and the community-level weighted means of trait values (CWM, expressing functional identity, Lavorel *et al.*, 2008). For the functional richness, we selected the *dbFD* option that offers the possibility to scale the FRic index. That means that the FRic at plot scale is standardized using the total FRic of the regional pool (i.e. all the species present within the study area) as a maximum. The consequence is that all FRic indices values are constrained between zero and one, which allows for comparisons between different sets of traits (e.g. the different disturbances). A value of one for FRic at the plot scale means that all the regional functional richness is present within this plot.

6.2.4. Traits and functional diversity analyses: overview

The analyses based on traits (Steps iv on Figure 6.2) are conducted at two temporal scales and two spatial scales (Figure 6.4). Each spatial scale is linked to an ecological level of organization. The local scale corresponds to the analysis of communities, which are local assemblages of species, whereas the regional scale

represents the woody vegetation in the landscape within the study area. The studied variables vary according to the ecological level and thus spatial scale. At the regional scale, we investigate the presence of species and traits values without considering species abundances. At the local scale, we focus on FD indices (which take account of species abundances). The analyses are presented in the two following sections (6.2.5 and 6.2.6) according to the temporal scale.

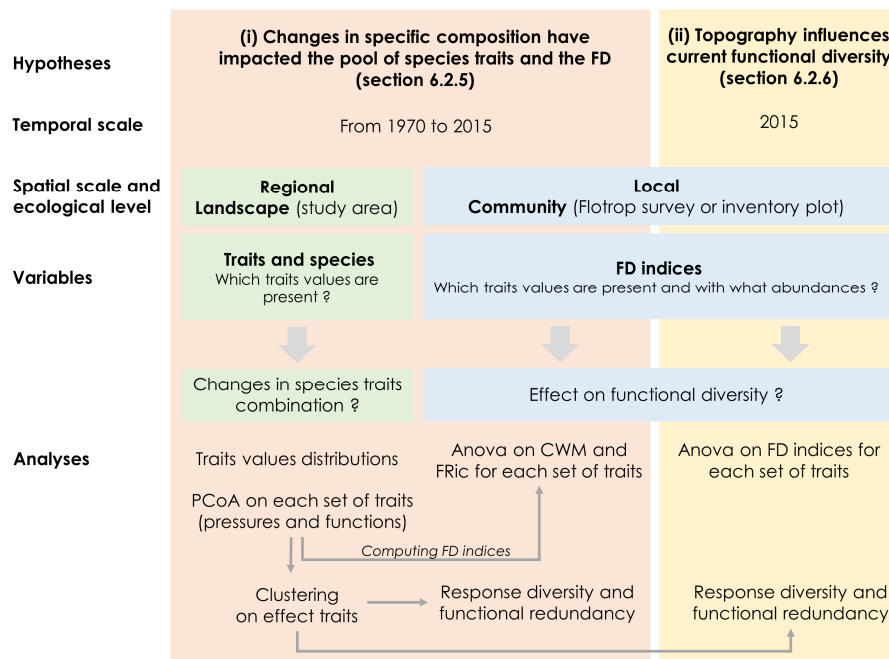


Figure 6.4 – Organization of the trait-based approach analyses (step iv from Figure 6.2) to test the two hypotheses, each of them linked to a temporal scale (from 1970 to 2015 and 2015). Two spatial scales (regional vs local) are also considered, each of them is linked to an ecological level of organization (landscape vs community).

In the first section (6.2.5), we evaluate changes from 1970 to 2015 in traits values at the regional scale (i.e. within the study area) and in FD indices at the local scale (community). We assume that from 1970 to 2015 the grazing pressure and the drought pressure have increased, given the occurrence of the great drought and the increase in livestock number (see section 3.2.4) and that it could have influenced the combinations of trait values present in the ecosystem. As for the fire pressure, monitoring of fires did not exist during the great drought. They might have been more frequent during the early years of the great drought and

might have decreased at the end of it because of the decrease in biomass, subsequent to the drought. Therefore, this pressure has been fluctuating during the three periods, not showing a linear increasing or decreasing trend.

At the regional scale (6.2.5.1), the distribution of traits values is examined to search for changes in mean traits values. We also perform Principal Coordinates Analyses (PCoA) on the five sets of traits for all the species present within the study area from 1970 to 2015. Finally, a hierarchical functional classification is applied for the two sets of effect traits in order to form functional effect groups. At the local scale (6.2.5.2), changes in functional diversity of communities are assessed via two FD indices: FRic and the CWM. We also compute functional redundancy and response diversity, based on our functional classification carried out at the regional scale.

In the second section (6.2.6), we focus on the influence of topography on the current FD (2015) through the analysis of five FD indices (FRic, FEve, FDiv, FDis, CWM); the functional redundancy; and on the response diversity.

6.2.5. Temporal changes in species traits and FD

6.2.5.1 Regional scale: species and traits

Trait values of the species present in the study area during the three periods (see 3.2.3.2), from 1970 to 2015, are considered at the regional scale without taking account of the species abundances. A preliminary exploratory analysis was carried out using a Principal Component Analysis (PCA) on the continuous traits to look at their correlation and see which traits most determine the distance between species. The traits are maximum height, wood density, vessel area, duration of leafing, leaf N content, leaf P content, leaf area, specific leaf area, seed weight, and fruit length. Missing values were replaced by dissimilarity function. This PCA is presented in Appendix 23.

Second, the distribution of the values of ten continuous traits (fruit length, maximum height, leaf area, leafing period, leaf N and P content, seed weight, SLA, vessel area and wood density) are examined for the three periods using density plot (i.e. a smoothed version of a histogram). The height of the curve corresponds to the estimated proportion (i.e. the estimated probability, not taking account of the species abundances) of species presenting that particular value of traits. The advantage over a histogram is that density plots do not depend on the number of breaks used to build the histogram.

Third, a Principal Coordinates Analysis (PCoA) was applied for each set of traits (including discrete and continuous traits) to visualize species in a multidimensional space. We determined which traits contributed the most to the PCoA axes. To do so, we performed linear regressions between species axes coordinates and species traits values (for continuous traits) whereas for categorical traits, we applied ANOVA to compare mean coordinates for each trait category.

Based on their frequency in Flotrop and in the inventory of 2015, we assigned to each species a “dynamic status” (Table 6.3). Species are qualified as rare (less than five occurrences in the set of inventory records); stable (stable frequencies or less than 10% of change), decreasing (more than 10% of decrease change) or increasing (see Chapter 5, Figure 5.8 for details). For statistical reasons, we regrouped the stable species with the increasing species, as it is impossible to draw conclusion based only on one species classified as “increasing”.

Table 6.3 – Reminder of the dynamic status of species (Figure 5.8). For species abbreviations, see Appendix 1.

Status	Species abbreviations
Rare	ACA, ACE, ACM, ACN, ANL, BAR, BRF, COS, ENA, FAA, FEA, GRF, LAA, MAA, MAS, MII, PIR, STK, SYG
Decreasing	ADO, ASN, ASY, COA, COG, COM, DAM, DIC, GRB, GUS, SCB, STS, TEA
Stable	ADD, BAA, BOS, CAP, LEP, ZIM
Increasing	ACT

Species dynamics status was outlined on the PCoA to see if this status depended on the combination of traits. Principal Coordinates Analyses on response traits allow discussing how the studied pressure has influenced the presence/absence of the species (filtering of the species) in the ecosystem (i.e. does the trajectory of a species through time depends on its traits combination for a particular pressure?). PCoA on effect traits illustrate the classification of species according to their effect on the studied functions and allow to see which of these functionalities are still present in the ecosystem.

Fourth, we performed a functional classification of the species using Ward’s hierarchical clustering method for the two effects traits (primary productivity and biogeochemical cycles functions), following Laliberté *et al.* (2010). The number of functional effect groups (FG) was visually determined on the dendrogram. The computation of FG allows first, to outline species with similar effect on

ecosystem functioning according to two functions studied and to assess functional redundancy. Second, it is the initial phase to study the response diversity (see section 6.2.5.2).

6.2.5.2 Local scale: FD of communities

Changes in functional diversity of communities (e.g. an inventory plot) from 1970 to 2015 are examined through two FD indices (FRic and CWM), functional redundancy and response diversity. The studied communities gather field inventory data from 2015 and a subset of the Flotrop database. We selected the records located inside a 20 km radius from the center of the study area and for which abundances (based on Braun-Blanquet coefficients) were available. These coefficients were transformed in relative abundances by dividing each abundance by the sum of the individual abundances. As in Chapter 5, we gathered the records in three periods (Table 6.4), according to their position relative to the great drought. However, we do not assume that the great drought is the key driver to all potential changes.

Table 6.4 – Number of inventory plots and Flotrop records (communities, separated according to the number of recorded species) available per climatic period.

	Before the great drought 1970-1971	During the great drought 1972-1986	After the great drought 2015
Less than 3 species	2	9	59
			4 depressions/55 tops
At least 3 species	76	40	80
			39 depressions/41 tops
<i>n</i> total	78	49	139

FRic and CWM were computed for the three periods and for each community and compared with Anova and Tukey test (see section 6.2.3 for the steps to compute these indices). We selected these two indices to assess changes in FD because the FEve, FDiv and FDis indices strongly depend on species abundances and their interpretation is less straightforward. Flotrop, while providing some rough estimation with Braun-Blanquet coefficient that differ from the abundance measurement made in our inventories, stays imprecise regarding these values. Besides, CWM, which expresses functional identity, is quite robust to the changes of methods for estimating abundances (Lavorel *et al.*, 2008; Taugourdeau, 2014). For the computation of FRic, we kept the plots with a species richness superior

or equal to three (Table 6.4). Indeed, functional richness index cannot be calculated with one or two species (Laliberté *et al.*, 2014; Villéger *et al.*, 2008). The consequence is that the mean FRic is biased upward, as the plots presenting the poorest species richness are discarded.

As functional redundancy and response diversity are two concepts within functional ecology that are involved in ecosystem resilience (see 6.1), we assessed them via an analysis that linked the two sets of effect traits with the three sets of response traits, following the methodology proposed by Laliberté *et al.* (2010). For each of the functional effect groups created in section 6.2.5.1, functional redundancy is measured as the number of species present within each functional effect group (Figure 6.5, left).

Response functional diversity (to drought, grazing or fire) of each functional effect group is assessed by its functional dispersion index (FDis; Laliberté and Legendre, 2010) measured in the response-traits functional space based on *response traits* (Figure 6.5, right; Chillo *et al.*, 2011; Laliberté *et al.*, 2010). FDis was unweighted by species abundances because minor species may contribute substantially to resilience as suggested by Walker *et al.* (1999). That means that the computation of the index assumes communities to have species with equals abundances.

A functional group (FG) that have a high dispersion in the response-traits space will contain species presenting a wide variety of responses to pressures. High dispersion within group therefore ensures the persistence of the FG under intensified pressures (Mori *et al.*, 2013). For a given FG, a decrease of FDis through time indicates that species within the group are now responding more similarly to pressures. This makes the group more at risk of disappearance in case of intensified pressure and therefore indicates a loss of resilience of the group (Laliberté *et al.*, 2010).

To compute FDis, the communities are partitioned in two or three “sub-communities” (according to the number of effect groups created) retaining species belonging to the clusters created. As communities in the study area generally present a low species richness, the partition increases the probability of having communities with no species for one of the effect group, which would make to computation of FDis impossible.

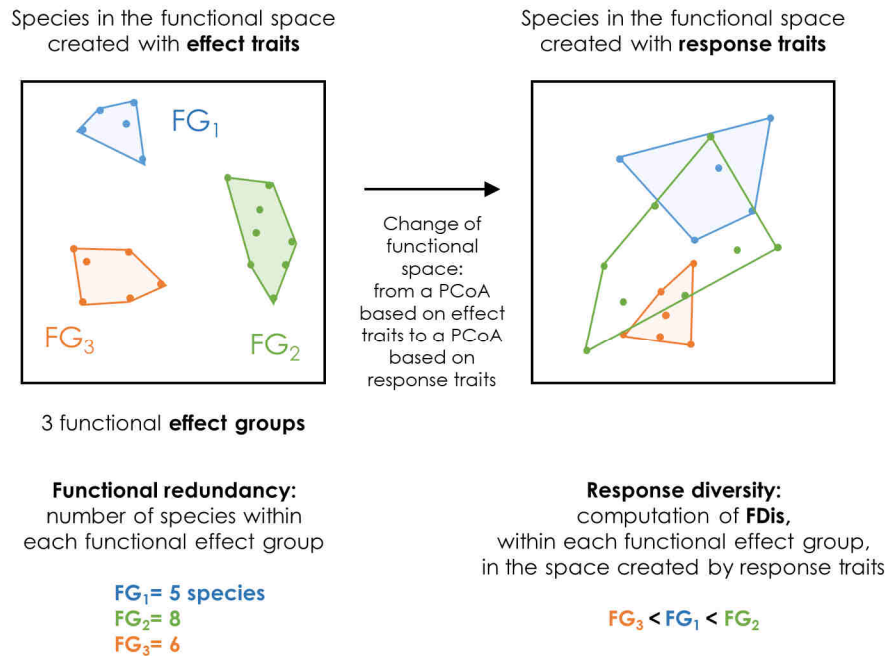


Figure 6.5 – Computation of functional redundancy and response diversity for a fictive community containing 19 species, represented by points. Left: the species are represented in the functional space created with effect traits (e.g. PCoA on the distance matrix based on effect traits). We can group them in three functional effect groups (FG). Functional redundancy is considered as the number of species within each group (5 species in FG_1 , 8 species in FG_2 and 6 species in FG_3). Right: the (same) species are represented in the functional space created with response traits (e.g. PCoA on the distance matrix based on response traits). Response diversity is assessed by the functional dispersion (FDis) of each functional effect group, calculated in the functional space created by response traits (FDis can be approximated by the mean distance to the center of the polygons). Response diversity of FG_3 is inferior to the response diversity of FG_1 and of FG_2 . We note that, while FG_1 has a lower functional redundancy, it possesses a higher response diversity than FG_3 .

To overcome this difficulty, we kept the number of effect groups to a minimum (two or three). In addition, we assigned a FDis value of zero to communities with no species. As indices between effect groups have to be compared, we used the first two axes of the PCoA on the response traits involving all species (and not only the ones belonging to the group) as new traits to compute FDis for each group. This way the differences between species considered are retained between effect groups. Each community thus presents for the two sets of effect traits, a

number of measures of response diversity corresponding to the number of effect groups multiplied by the number of response sets (i.e. three). For instance, an inventory plot will have nine values of response diversity for the biogeochemical function if three functional effect groups are created (3 FG x 3 disturbances). Each community also presents a number of functional redundancy measures corresponding to the number of effects groups.

6.2.6. Influence of topography on current functional diversity

The influence of topography on current functional diversity is studied using field data from 2015. Indeed, contrary to the historical field data (Flotrop), we possess information on the plots topography. The computation of FD indices (FRic, FEve, FDiv, FDis and CWM) for each pressure and function followed the steps described in section 6.2.3. FD indices were then compared for each topographic element (tops vs depressions) using Wilcoxon tests. For the analysis of four indices (FRic, FEve, FDiv and FDis), we kept the plots with a species richness superior or equal to three ($n = 80$, 39 depressions and 41 tops) for the same reason as explained in 6.2.5.2.

The assessment of functional redundancy and response diversity is based on the same functional classification presented in section 6.2.5.1 and relies on the same methodology as described in section 6.2.5.2. Functional redundancy and response diversity of each functional effect group were compared for communities located on tops and in depressions.

6.3. Results

6.3.1. Trait matrix from literature review

Traits values gathered from the literature are in Table 6.5 for the 39 species, formerly or currently present within our study area. We do not comment on these traits values, as they will be discussed across our following analyses. We remind here that the values have been simplified in order to take account of the potential differences according to the sources (see section 3.3.4 for the rules that were applied).

Table 6.5 – Traits values for 39 species recorded in 2015 or in Flotrop (from 1970 to 1986). See Appendix 1 for species abbreviations and Table 6.1 for the traits abbreviations. Empty cells indicate missing values for the trait (no information was found in the literature).

Species	Whole-plant traits			Leaf traits				
	form	h.max	spin	pr.dig	lf.arc	lf.siz	lf.per	lf.mth
ACA	bush	10	2	4.4	1160	submicroph.	deciduous	
ACE	bush	10	2				deciduous	5.0
ACM	bush	8	2	12.0			deciduous	6.0
ACN	tree	20	3	8.0			deciduous	4.5
ASN	bush	12	2	17.1	970	microph.	deciduous	7.0
ASY	tree	17	3	13.0	180	nanoph.	deciduous	7.5
ACT	tree	21	4	12.0	260	microph.	semi-evergreen	11.0
ADD	tree	25	1	7.5	7830	mesoph.	deciduous	5.0
ADO	bush	4	1		1030	submicroph.	deciduous	5.0
ANL	tree	30	1	5.8		submicroph.	deciduous	9.0
BAA	tree	9	4	8.4	540	microph.	evergreen	12.0
BAR	bush	8	2	8.8		microph.	deciduous	
BOS	shrub	5	1	16.8	1000	submicroph.	evergreen	12.0
BRF	bush	8	1				deciduous	5.0
CAP	shrub	5	1		14130	mesoph.	evergreen	12.0
COA	bush	4	2	10.5	300	microph.	deciduous	6.0
COG	tree	12	1	7.5	2500	mesoph.	evergreen	12.0
COM	bush	6	2	8.8	360	microph.	deciduous	4.0
COS	bush	6	1				deciduous	
DAM	tree	10	2	16.4			deciduous	2.0
DIC	bush	7	3	12.3	1660	submicroph.	deciduous	6.0
ENA	tree	12	1	18.3			deciduous	4.0
FAA	tree	20	3	10.0	220	microph.	deciduous	9.5
FEA	bush	6	1	5.4	720	submicroph.	deciduous	7.0
GRB	bush	8	1	7.0	840	submicroph.	deciduous	6.0
GRF	bush	8	1		270	microph.	deciduous	
GUS	bush	5	1	8.9	550	microph.	semi-evergreen	11.0
LAA	tree	12	1		1700	submicroph.	deciduous	8.0
LEP	shrub	3	1			nanoph.	evergreen	12.0
MAA	tree	10	1				deciduous	
MAS	tree	8	3	1.6			deciduous	12.0
MII	bush	10	1	10.5			evergreen	12.0
PIR	tree	10	1	6.2			semi-evergreen	12.0
SCB	tree	12	1	4.7	3530	mesoph.	deciduous	7.0
STS	tree	18	1	0.0	6660	mesoph.	deciduous	5.0
STK	tree	12	1	3.4		mesoph.	deciduous	2.0
SYG	tree	15	1			mesoph.	evergreen	12.0
TEA	tree	10	1	5.7		mesoph.	deciduous	11.0
ZIM	tree	16	2	10.4	550	microph.	semi-evergreen	10.0

Table 6.5 – continued.

Species	Leaf traits (continued)			Stem traits			Below-ground traits	
	lf.N	lf.P	N.fix	N.fix	vs.arc	wd.den	N.fix	taprt
ACA	28.4	1.6	yes	yes	0.0131	0.69	yes	
ACE			yes	yes	0.0197	0.74	yes	
ACM		1.7	yes	yes	0.0197	0.74	yes	
ACN	21.0	1.2	yes	yes	0.0055	0.74	yes	1
ASN	37.4	2.2	yes	yes	0.0067	0.76	yes	1
ASY	25.3	2.2	yes	yes	0.0197	0.71	yes	1
ACT	28.0	2.0	yes	yes	0.0113	0.74	yes	1
ADD	21.9	2.5	no	no	0.0452	0.28	no	0
ADO			no	no			no	
ANL	18.0	1.2	no	no	0.0044	0.97	no	
BAA	20.0	1.0	no	no	0.0091	0.70	no	1
BAR	23.0	1.5	no	no	0.0044	0.67	no	1
BOS	34.0	1.5	no	no		0.69	no	0
BRF						0.55		
CAP	20.9	1.5	no	no	0.0078		no	1
COA	26.0	2.2	no	no		0.70	no	
COG	17.0	2.0	no	no		0.84	no	
COM	22.0	1.7	no	no		0.42	no	0
COS					0.0095	0.51		
DAM	33.3	1.8	yes	yes	0.0133	1.21	yes	1
DIC	26.0	2.0	yes	yes	0.0154	0.86	yes	
ENA		2.2	yes	yes	0.0491	0.52	yes	
FAA	25.0	2.0	yes	yes	0.0363	0.60	yes	1
FEA	25.0	1.4	no	no		0.66	no	
GRB	23.0	1.5	no	no	0.0024	0.76	no	0
GRF	28.5	1.3	no	no	0.0024	0.69	no	
GUS	20.0	1.8	no	no		0.67	no	1
LAA	15.5	1.0	no	no		0.46	no	
LEP			no	no			no	1
MAA	37.0				0.0018	0.90		
MAS		0.6				0.71		
MII		1.6			0.0087	0.58		
PIR	24.0	2.0	no	no		0.65	no	1
SCB	20.0	1.5	no	no		0.54	no	1
STS	21.5	0.5	no	no		0.31	no	
STK	19.0	0.5	no	no	0.0107	0.60	no	
SYG	16.1		no	no		0.60	no	
TEA	15.0	1.2	no	no		0.64	no	
ZIM	23.0	1.8	no	no	0.0123	0.60	no	1

Table 6.5 – continued.

Species	Regenerative traits				
	disp	fr.lg	cop	rt.suc	sd.w
ACA	anemochorous	85	yes	yes	75
ACE	anemochorous	125	yes	no	90
ACM	anemochorous	95	yes	no	70
ACN	zoochorous	125	yes	yes	130
ASN	anemochorous	90	yes	no	55
ASY	zoochorous	135	yes	yes	45
ACT	zoochorous	95	yes		50
ADD	zoochorous	300	yes	no	1000
ADO	anemochorous				20
ANL	anemochorous	5	no	yes	10
BAA	zoochorous	50	yes	yes	1300
BAR	zoochorous	75	yes	yes	90
BOS	zoochorous	12	yes	no	300
BRF	zoochorous	7	yes	no	50
CAP	anemochorous	75	yes		10
COA	anemochorous	19	yes	no	60
COG	anemochorous	32	yes		65
COM	zoochorous	7	yes	yes	125
COS	zoochorous				100
DAM	anemochorous	45	yes	no	80
DIC	zoochorous	65	yes	yes	20
ENA	anemochorous	275	no	no	225
FAA	zoochorous	125	yes	yes	70
FEA	zoochorous	6	yes	yes	10
GRB	zoochorous	5	yes	no	90
GRF	zoochorous	10	yes		120
GUS	anemochorous	37	yes	yes	30
LAA	zoochorous	10	no	no	130
LEP	anemochorous				5
MAA	zoochorous	250			120
MAS	zoochorous				
MII	anemochorous	5	yes	yes	1
PIR	zoochorous	200	yes	yes	80
SCB	zoochorous	33	yes		2250
STS	zoochorous	80	no	no	350
STK	anemochorous	500	yes	yes	30
SYG		10	yes		2220
TEA	anemochorous	57	yes	no	330
ZIM	zoochorous	13	yes	yes	290

6.3.2. Temporal changes

6.3.2.1 Regional scale: species and traits

The distribution of ten continuous traits (i.e. the repartition of the trait values at the regional scale) are represented in Figure 6.6 on density plots. The distributions are quite similar for the three periods, meaning that the distribution of the values (the number of species per trait value) have stayed the same during the three periods. In some cases (fruit length, leafing period, leaf P content, seed weight), we observe a shift in the medians and/or means between the first and the second period, before returning to its original value in the third period.

The PCoA on drought response traits (Figure 6.7) reveals a clear break between stable species and the others. Stable species are all in the upper right quadrant, with the exception of *Adansonia*. Anova and Tukey test on the second axis coordinates reveal a significant difference ($P < 0.01$) between decreasing species and stable ones. This suggests that drought has filtered the species, from 1970 to 2015, allowing the persistence of a unique set of trait values (i.e. strategy). This strategy is characterized by the traits combination of a long leafing period, small vessel area and heavy seeds. *Adansonia* does not, however, present the same traits combination than the six other stable species. It is closer from *Sclerocarya*, which belongs to the decreasing species.

On the PCoA for the fire response, we can see that species are separated in two large clusters, according to the first axis (Figure 6.8). The separation is based on the species dispersal mode. The right side the plot gathers the species dispersed by animals whereas the species dispersed by wind are on the left side. As there are stable species in both groups, this trait does not appear to determine whether the species will persist or not. *Calotropis* and *Leptadenia* are located far away from the other stable species, probably due to their dispersal mode (by wind).

Species are also separated according to the first axis on the PCoA for grazing response (Figure 6.9), though in a lesser extent than for the PCoA on fire response traits. Species on the right side are more often zoochorous and species on the left side anemochorous. Contrary to the PCoA for drought, stable species are not separated from the decreasing species on the PCoA for fire and grazing response.

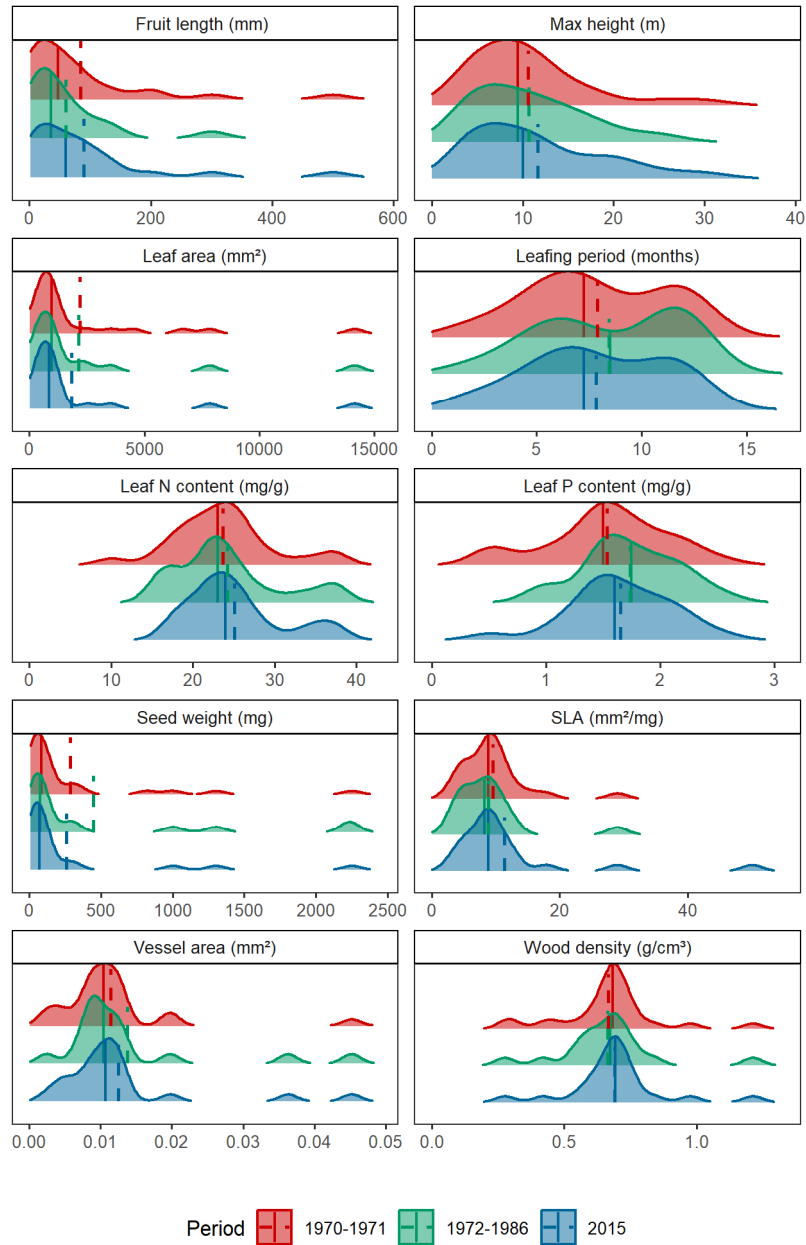


Figure 6.6 – Kernel density estimates of 10 continuous traits for the three periods: before the great drought (1970-1971, from Flotrop); during the great drought (1972-1986, from Flotrop); and after the drought (2015; field data). Means and medians of the distributions are in dashed lines and solid lines respectively.

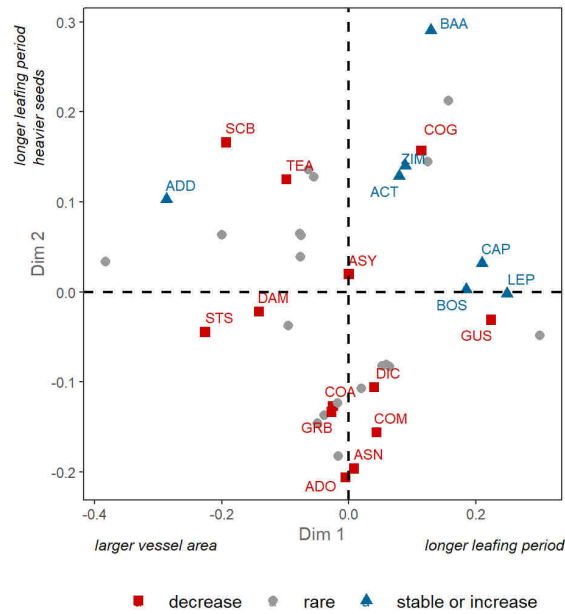


Figure 6.7 – Principal Coordinates Analysis on drought response traits. Traits that significantly influence the axes are indicated in *italic*, on the respective sides of the axes. Colors and shapes refer to the “dynamics status” of species. For the sake of clarity, we only labeled the stable and decreasing species.

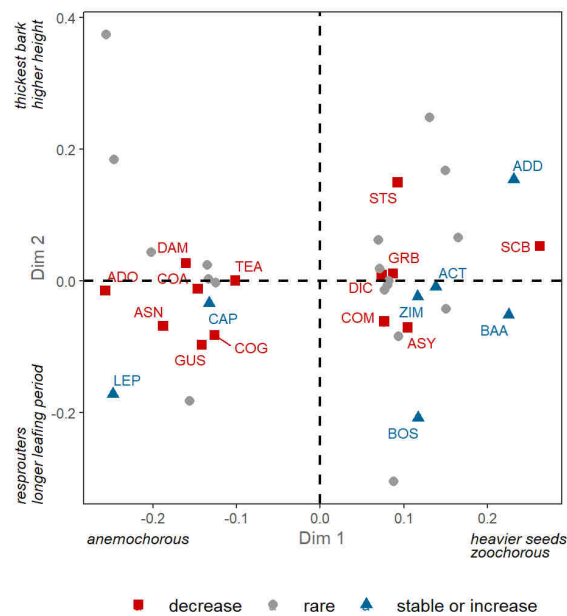


Figure 6.8 – PCoA on fire response traits. Same legend as Figure 6.7.

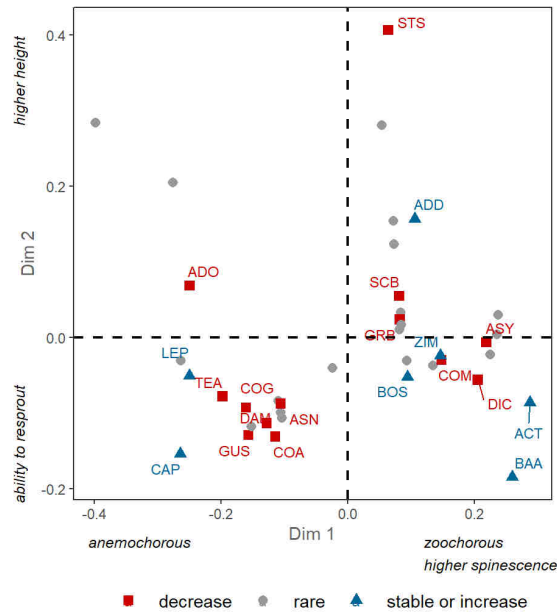


Figure 6.9 – PCoA on grazing response traits. Same legend as Figure 6.7.

The Principal Coordinates Analysis on the effect traits for the primary productivity also shows two groups of species, separated by the first axis (Figure 6.10.a). The traits that influence the first axis are the maximum height and the leaf N content. The second axis mainly expresses the wood density, the leaf N content and the leaf area.

The hierarchical clustering confirms the two functional effects groups (FG-pp1 and FG-pp2, Figure 6.10.b) of the same size (19 and 20 species). The first functional group of primary productivity (FG-pp1) gathers bushes and shrubs with a higher leaf N content (e.g. *Boscia senegalensis*, *Bauhinia rufescens*) than the species of the second FG (FG-pp2), which are only trees (e.g. *Acacia seyal*, *Acacia tortilis*, *Balanites aegyptiaca*, *Sclerocarya birrea*). As there are stable species in both groups, we can assume that the current ecosystem still presents these two main functionalities, while losing some “minor” functionalities (due to the decreasing species) among the continuum of these effects.

The first axis of the PCoA for the biogeochemical cycles separates the species according to the values of their height and leafing period and their ability to resprout and to fix nitrogen (Figure 6.11, a). The second axis reflects the traits of the duration of leafing period, leaf P and N content and the ability to fix nitrogen.

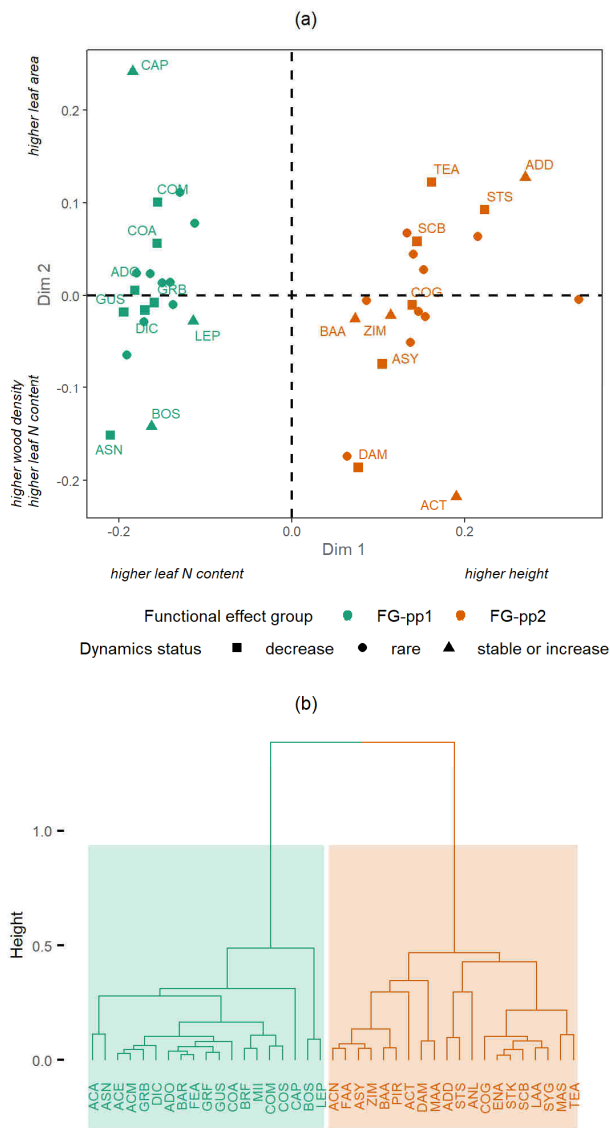


Figure 6.10 – Functional effect groups for primary productivity (FG-pp). (a) Principal Coordinates Analysis on the primary productivity effect traits. Traits that significantly influence the axes are indicated in *italic*, on the respective sides of the axes. Shapes refer to the “dynamics status” of species and colors refer to the functional groups. For the sake of clarity, we only labeled the stable and decreasing species. (b) Dendrogram of the hierarchical classification (using Ward’s method), using the same colors for groups as on the PCoA.

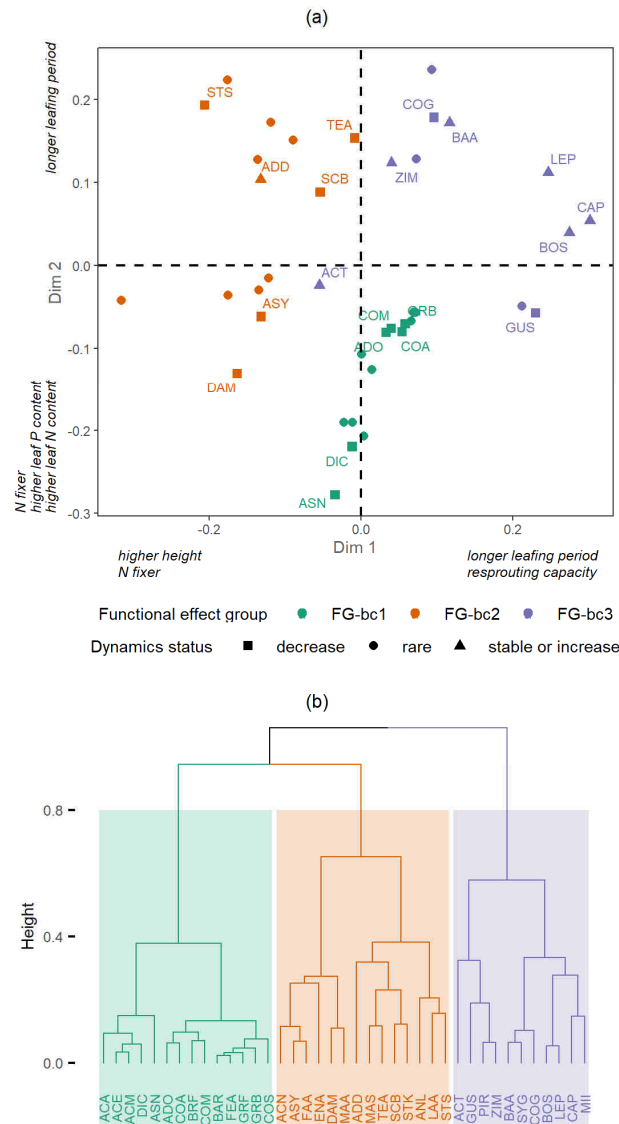


Figure 6.11 – Functional effect groups for biogeochemical cycles. (a) Principal Coordinates Analysis on the biogeochemical cycles effect traits. Traits that significantly influence the axes are indicated in *italic*, on the respective sides of the axes. Shapes refer to the “dynamics status” of species and colors refer to the functional groups. For the sake of clarity, we only labeled the stable and decreasing species. (b) Dendrogram of the hierarchical classification (using Ward’s method), using the same colors for groups as on the PCoA.

Three FG (FG-bc1, FG-bc2, FG-bc3), containing 14, 14 and 11 species, were created for the biogeochemical cycles (Figure 6.11, b). The traits responsible for this clustering are height, leaf phenology and N fixation ability. Small deciduous species form the first FG (FG-bc1, e.g. *Grewia bicolor*, *Commiphora africana*), taller deciduous species are in the second FG (FG-bc2, e.g. *Acacia seyal*, *Sclerocarya birrea*) and the third FG gathers mainly evergreen or semi-evergreen non-fixer species (FG-bc3, e.g. *Balanites aegyptiaca*, *Boscia senegalensis*), except for *Acacia tortilis*. While FG-bc3 is mainly constituted by abundant and stable species, FG-bc1 and FG-bc2 mostly gather rare and decreasing species.

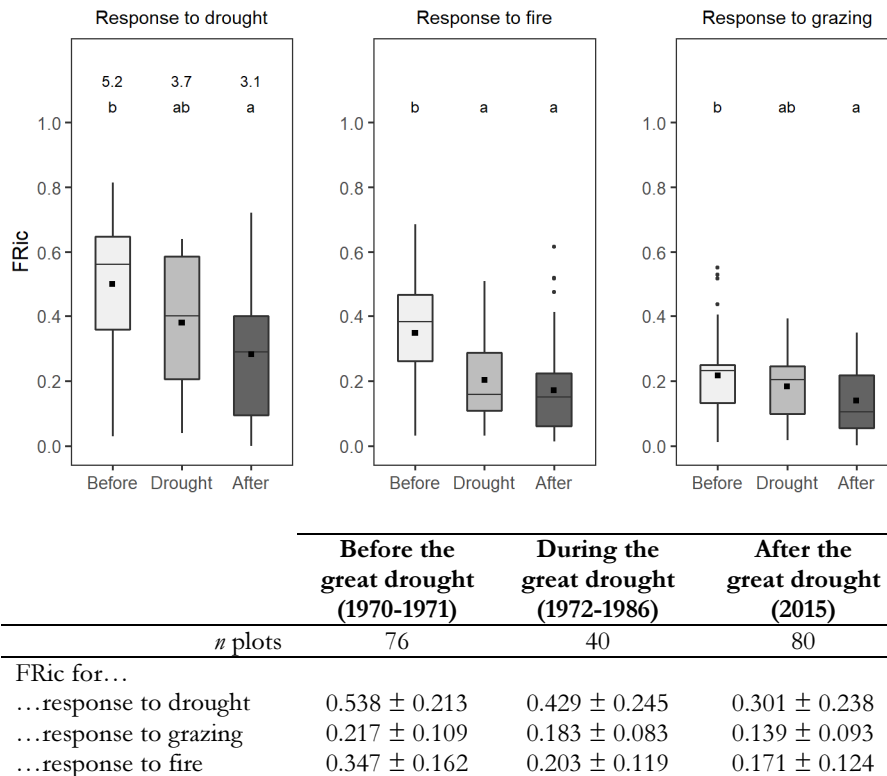


Figure 6.12 – Functional richness dynamics for the three disturbances (sets of response traits; *n* plots = 196). The means are represented by the squares. The numbers above the boxes on the first plot give the mean specific richness by record per period. The letters indicate the differences according to the Wilcoxon's tests between period with p-value adjustment ($P < 0.01$).

6.3.2.2 Local scale: temporal changes in FD

Mean functional richness (FRic) of woody communities (i.e. local scale) has clearly decreased, for the three sets of response traits, from before to after the great drought (Figure 6.12). This general decrease in functional richness is combined with a decrease in taxonomic (specific) richness, as the mean species richness for a record before 1970 is of 5.2 species and falls to 3.1 species for a record after the great drought. We also observe that the range of FRic indices is tighten starting from the second period. This narrowing comes from a decrease in the FRic value of the richest communities. Indeed, the presence of poor functional communities (i.e. with a small FRic, lower whisker) is attested before and after the great drought whereas the maximum values for FRic (upper whisker) decrease through time.

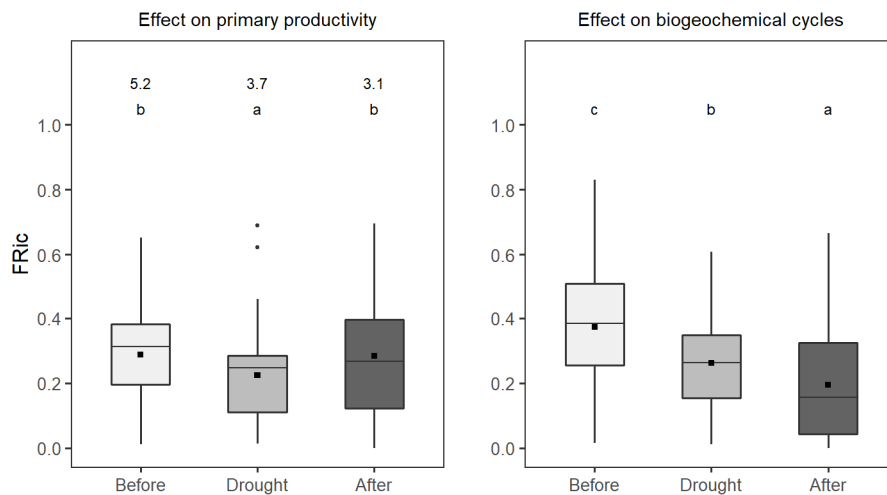
The taxonomical diversity strongly decreased between the first two periods (proportionally more than from period 2 to 3). However, this decrease is not immediately reflected in the FD for drought response, as FRic steepest decline is between period 2 and 3 (mean FRic from 0.43 to 0.30). It is the same for grazing response, as the mean FRic is significantly different between period 1 and 3 (and not between period 1-2 or 2-3). For the fire response however, the decrease in functional richness is immediate during the great drought, as the means of the first and the second period are significantly different.

The observed decline for the three responses might actually be sharper. Indeed, plots with less than three species were discarded from the analysis and we note that there are much more plots with that characteristic in 2015 (59 out of 139) than in 1970-1971 (2 out of 78) or in 1972-1986 (9 out of 49; Table 6.4).

The average FRic for the primary productivity dropped from 0.29 before the great drought to 0.22 during the drought, followed by a recovery after the drought (mean FRic of 0.28; Figure 6.13). FRic for the effect on biogeochemical cycles has decreased both in its average and in its range (lower and upper whiskers). The richest communities after the great drought present a FRic around 0.6, compared to 0.8 before the drought.

Changes in FD are also marked for the community-weighted means of continuous traits with the exception of fruit length, which remains stable from 1970 to 2015 (Figure 6.14 and Table A24.1 in Appendix 24). The changes are more abrupt between the second and the third period, following the same pattern as for FRic, with a latency period between the great drought and its consequences. Indeed, for all CWM (except for fruit length), the means are

significantly different between the first and the third period but not between the first and the second.



	Before the great drought (1970-1971)	During the great drought (1972-1986)	After the great drought (2015)
<i>n</i> plots	76	40	80
FRic for the effect on primary productivity	0.287 ± 0.140	0.225 ± 0.151	0.283 ± 0.198
FRic for the effect on biochemical cycles	0.373 ± 0.168	0.262 ± 0.148	0.194 ± 0.171

Figure 6.13 – Functional richness dynamics for the two functions (sets of effect traits, *n* plots = 196). The means are represented by the squares. The numbers above the boxes on the first plot give the mean specific richness by record per period. The letters indicate the differences according to the Wilcoxon's tests between period with p-value adjustment ($P < 0.01$).

The average CWM of maximum height falls from 10 m before the great drought to 8.1 m after. Tall trees that were still present during the great drought are scarce in the current communities. We also observe a change in leaf persistence, with the current dominance of semi-evergreen and evergreen species (mean CWM from 9 to 11 months). The mean CWM of seed weight also decreased significantly from more than 1100 mg to 660 mg. CWM of wood density and vessel area show that species with harder wood (from 0.63 to 0.68 g.cm⁻³) and smaller vessel area (from 0.0105 to 0.0094 mm²) are more frequent in the current

ecosystem. The average CWM of SLA considerably increased from 5.3 to 9.49 mm².mg⁻¹.

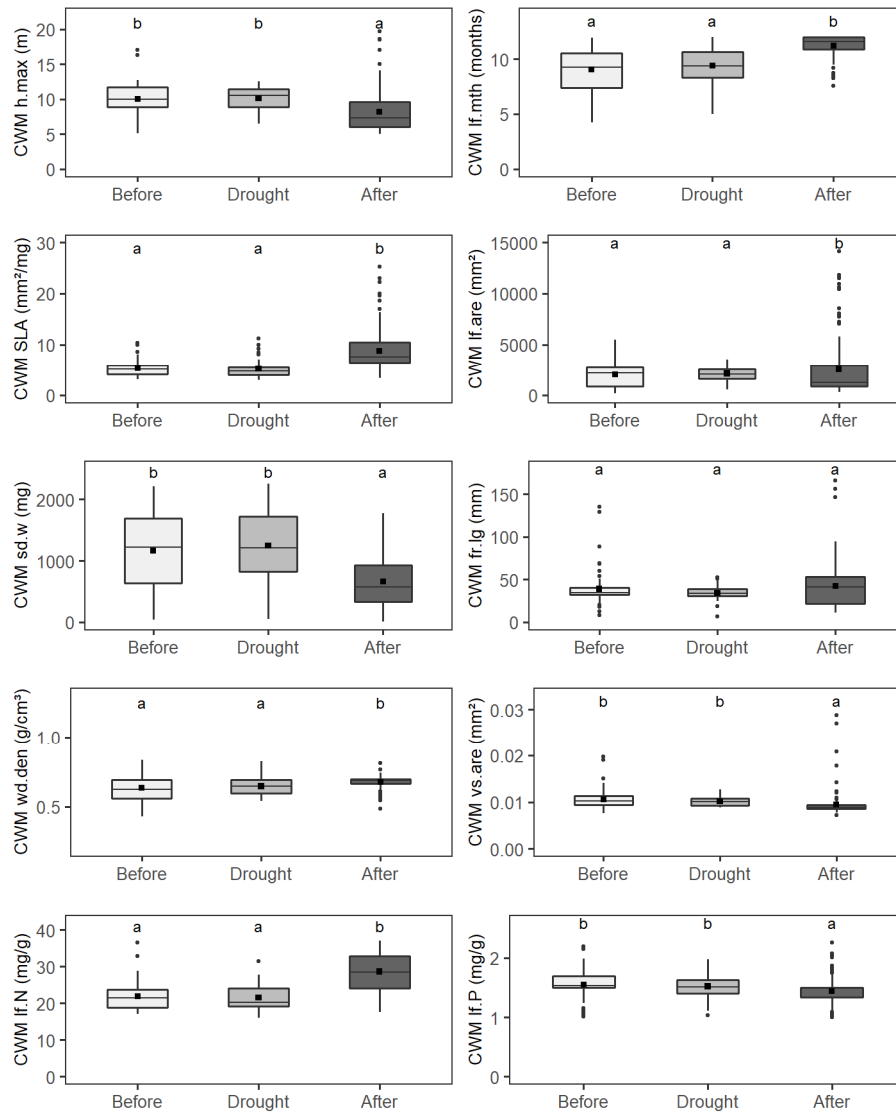
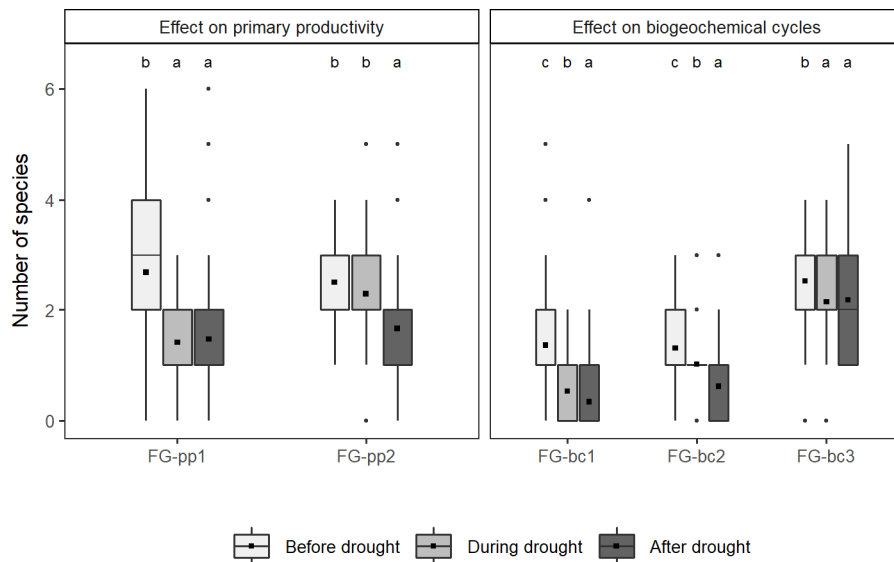


Figure 6.14 – Changes in CWM(expressing functional identity) of (from top-left to bottom-right) maximum height, leafing period, SLA, leaf area, seed weight, fruit length, wood density, vessel area, leaf nitrogen content and leaf phosphorus content ($n = 266$ plots; 78 in 1970-1971, 49 in 1972-1986, and 139 in 2015). The means are represented by the squares. The letters indicate the differences according to the Wilcoxon's tests between period with p-value adjustment ($P < 0.01$).

In addition to the shift in means, changes in the distribution can also be observed with a decrease in the interquartile range for the CWM of leafing period, wood density and vessel area. We can assume that the communities are becoming more homogeneous (from one community to another) for these traits. The opposite phenomenon occurs for the CWM of SLA, leaf N content and fruit length, with a higher interquartile range after the great drought.

The evolution of functional redundancy from before to after the great drought are illustrated in Figure 6.15. The overall pattern highlights a decrease in mean functional redundancy for the two functions in all functional groups.



	Before the great drought (1970-1971)	During the great drought (1972-1986)	After the great drought (2015)
<i>n</i> plots	78	49	139
FG-pp1	2.7 ± 1.5	1.4 ± 0.9	1.4 ± 1.1
FG-pp2	2.5 ± 0.8	2.3 ± 0.9	1.6 ± 1.1
FG-bc1	1.4 ± 1.1	0.5 ± 0.6	0.3 ± 0.6
FG-bc2	1.3 ± 0.6	1.0 ± 0.6	0.6 ± 0.6
FG-bc3	2.5 ± 0.9	2.1 ± 0.9	2.1 ± 1.1

Figure 6.15 – Evolution of the functional redundancy (number of species) in each effect group for primary productivity (FG-pp) and biogeochemical cycles (FG-bc). The means are represented by the squares. The letters indicate the differences according to the Wilcoxon's pairwise tests ($P < 0.05$) within each group.

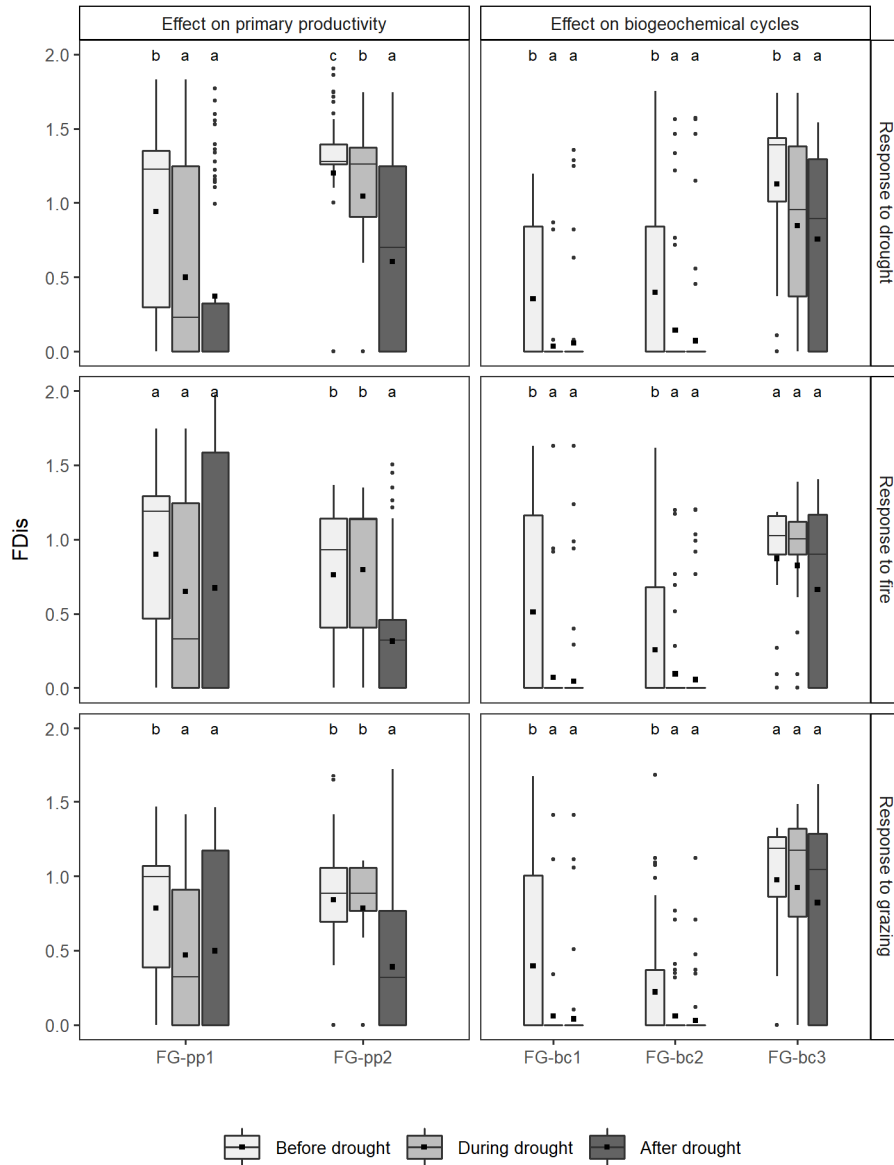


Figure 6.16 – Evolution of response diversity (to the three studied pressures) in each functional effect group of primary productivity and biogeochemical cycles ($n = 266$ plots; 78 in 1970-1971, 49 in 1972-1986, and 139 in 2015). The letters indicate the differences according to the Wilcoxon's pairwise tests ($P < 0.05$).

For primary productivity, mean redundancy of FG-pp1 declined directly after the great drought, from 2.7 to 1.4, before stabilizing in 2015. For FG-pp2, the fall is

marked from the second to the third period, from a mean redundancy of 2.5 in 1970-1971, to 2.3 in 1972-1986 and finally to 1.6 in 2015.

For biogeochemical cycles, mean redundancy of FG-bc1 and FG-bc2 show a continuous decrease from 1970 to 2015. They shift from 1.4 (1970-1971) to 0.5 (1972-1986) to 0.3 (2015) for FG-bc1 and from 1.3, to 1, to 0.6 in 2015 for FG-bc2. Mean redundancy for FG-bc3, while decreasing from 2.5 (1970-1971) to 2.1, presents a stabilization after the great drought.

The evolution of response diversity (FDis indices) follows more or less the same pattern for all FG, regardless of the effect or response set (Figure 6.16, see Table A24.2 in Appendix 24 for means and standard deviations).

Response diversity to drought of the five FG present a decline during the great drought, followed by a stabilization, except for FG-pp2 that continues to decrease after the great drought. Mean response diversity shifts from 0.94 (1970-1971) to 0.37 (2015) for FG-pp1 and from 1.2 (1970-1971) to 0.6 (2015) for FG-pp2. For biogeochemical cycles, mean response diversity of FG-bc1 and FG-bc2 is close to zero after the great drought.

Changes in response diversity to fire are less marked. The values of FG-pp1 and FG-bc3 stay similar during the three periods. Response diversity of FG-pp2 decreases after the great drought from 0.79 in 1972-1986 to 0.39 in 2015. As for FG-bc1 and FG-bc2, they present a response diversity to fire (and to grazing) close to zero starting from the second period.

Response diversity to grazing presents the same trends as the response diversity to drought with two exceptions: FG-pp2, for which the decrease stops between 1972-1986 and 2015 and FG-bc3, for which mean response diversity do not change from 1970 to 2015

6.3.3. Influence of topography on current functional diversity

We present here the results of functional diversity in 2015 at the community scale, meaning that FD indices are calculated for local assemblages of species belonging to the inventory plots of 2015. Species abundances are taken into account, via the computation of FD indices (except for FRic index).

Figure 6.17 illustrates the differences for the four FD indices (FRic, FEve, FDiv and FDis) between tops and depressions for the three sets of response traits and

the two sets of effect traits. Mean functional richness is significantly higher for the plots located inside depressions for the response to drought, to grazing and for both sets of effect traits (Wilcoxon's tests, $P < 0.01$). Mean FRic for fire response is also higher for the communities in depressions, though not significantly (Figure 6.17 and Table A25.1 in Appendix 25).

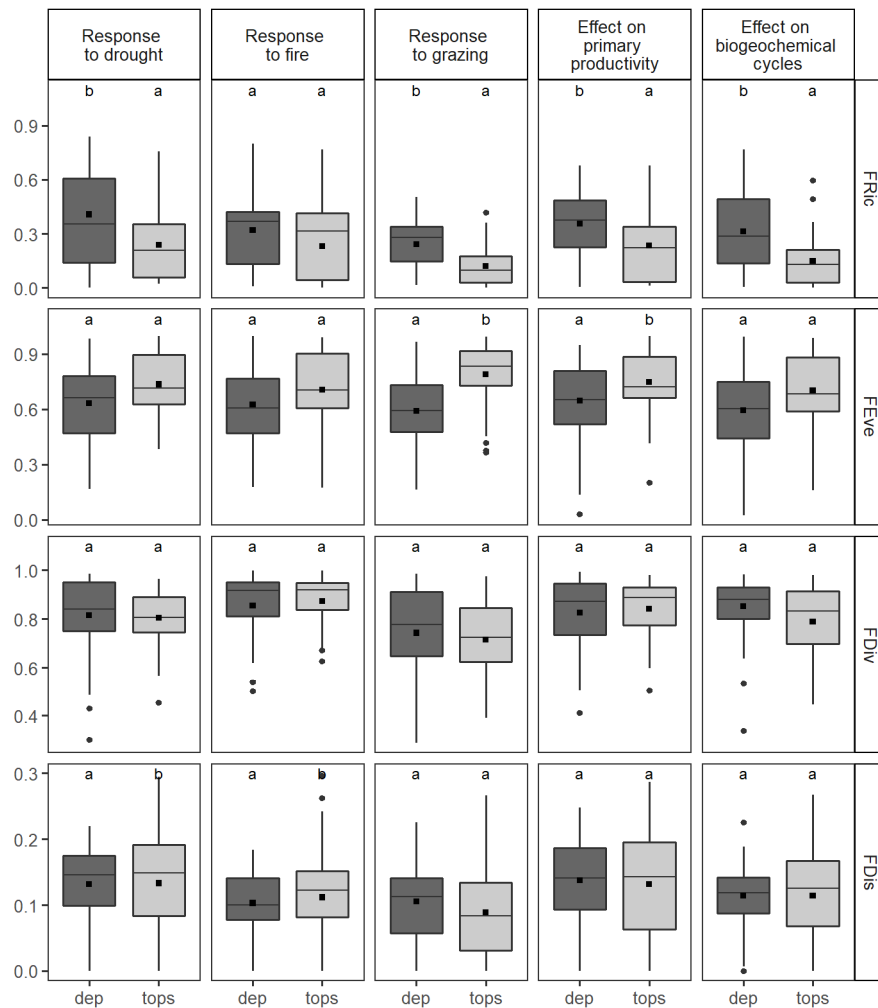


Figure 6.17 – Influence of topography on four FD indices ($n = 139$ plots): FRic, FEve, FDiv and FDis for the three sets of response traits (disturbances) and the two sets of effect traits (functions). The solid lines inside the boxes represent the medians and the squares represent the means. Letters indicate if the means are significantly different according to the Wilcoxon's tests ($P < 0.01$).

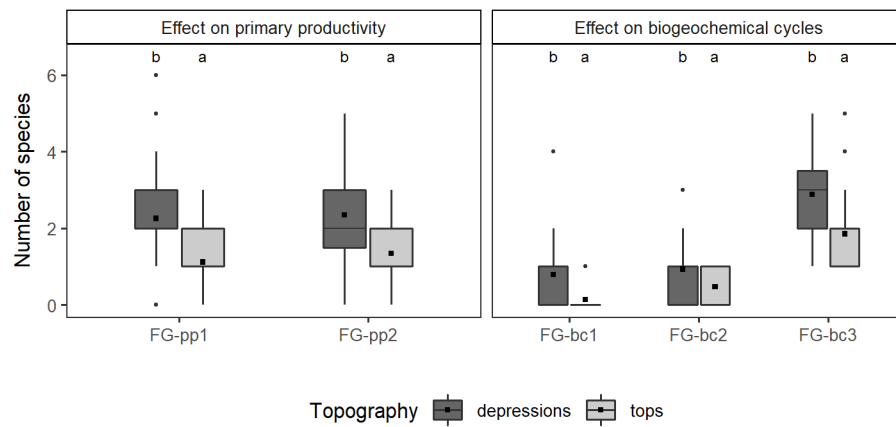
Mean functional evenness is superior on tops for two sets over five: the response to grazing and the effect on primary productivity. Mean functional divergence for the three responses and the two effects shows no significant differences between the two topographic elements whereas mean functional dispersion is higher on tops for drought and fire response (Figure 6.17 and Table A25.1 in Appendix 25).

The topography has no effect on the mean CWM (see Table A25.2 and Figure A25.1 in Appendix 25). It means that, on average, a mean individual (i.e. an individual randomly selected, regardless of the species) from a community located in depressions would present similar values for the 10 continuous traits.

Mean functional redundancies (number of species in each FG) of FG-pp1 and FG-pp2 are similar (1.5 and 1.6) if the topography is not taken into account ($P > 0.05$). For biogeochemical cycles, FG-bc3 presents a mean functional redundancy (2.2) significantly higher than FG-bc2 (0.6), whose functional redundancy is slightly higher than FG-bc1 (0.3; $P < 0.05$).

When considering the topography, depressions present a higher redundancy for all FG (Figure 6.18). The balance between the two FG-pp is maintained on each topographic element (2.2, 2.3 for FG-pp1 and FG-pp2 in depressions; 1.1 for FG-pp1, 1.3 for FG-pp2 on tops). The redundancy of biogeochemical cycles FG present large differences between each other. FG-bc3 is the group with higher redundancy on both topographic elements (2.9 and 1.8 for the depressions and tops, respectively). FG-bc1 presents a mean redundancy that is close to zero in communities located on tops.

Mean response diversity to the three pressures (FDis in response-traits space) for the five FG is represented in Figure 6.19 (see Table A25.3 in Appendix 25 for means and standard deviations of FDis). Mean FDis of each FG (whatever the set of traits) are significantly lower on tops compared to depressions. For the primary productivity function, response diversity levels across groups change according to the response set considered. Response diversity to drought is higher in FG-pp2 (0.62 and 0.42 for depressions and tops respectively) than in FG-pp1 (0.31 and 0.10). The trend is reversed for the responses to fire and grazing, with a higher mean FDis in FG-pp1 than for FG-pp2. For the biogeochemical cycles function, mean response diversity to the three responses in FG-bc3 is highly superior to the response diversity of FG-bc1 and FG-bc2, whose values are near zero in depressions and equal to zero on tops.



FG	Depressions	Tops
FG-pp1	2.2 ± 1.4	1.1 ± 0.8
FG-pp2	2.3 ± 1.2	1.3 ± 0.8
FG-bc1	0.8 ± 0.9	0.1 ± 0.3
FG-bc2	0.9 ± 0.8	0.5 ± 0.5
FG-bc3	2.9 ± 1.0	1.8 ± 0.9

Figure 6.18 – Functional redundancy (number of species) in each functional effect group of primary productivity (FG-pp) and biogeochemical cycles (FG-bc) according to the topography ($n = 139$ plots). The means are represented by the squares. The letters indicate the differences between topographic elements according to the Wilcoxon's tests ($P < 0.05$).

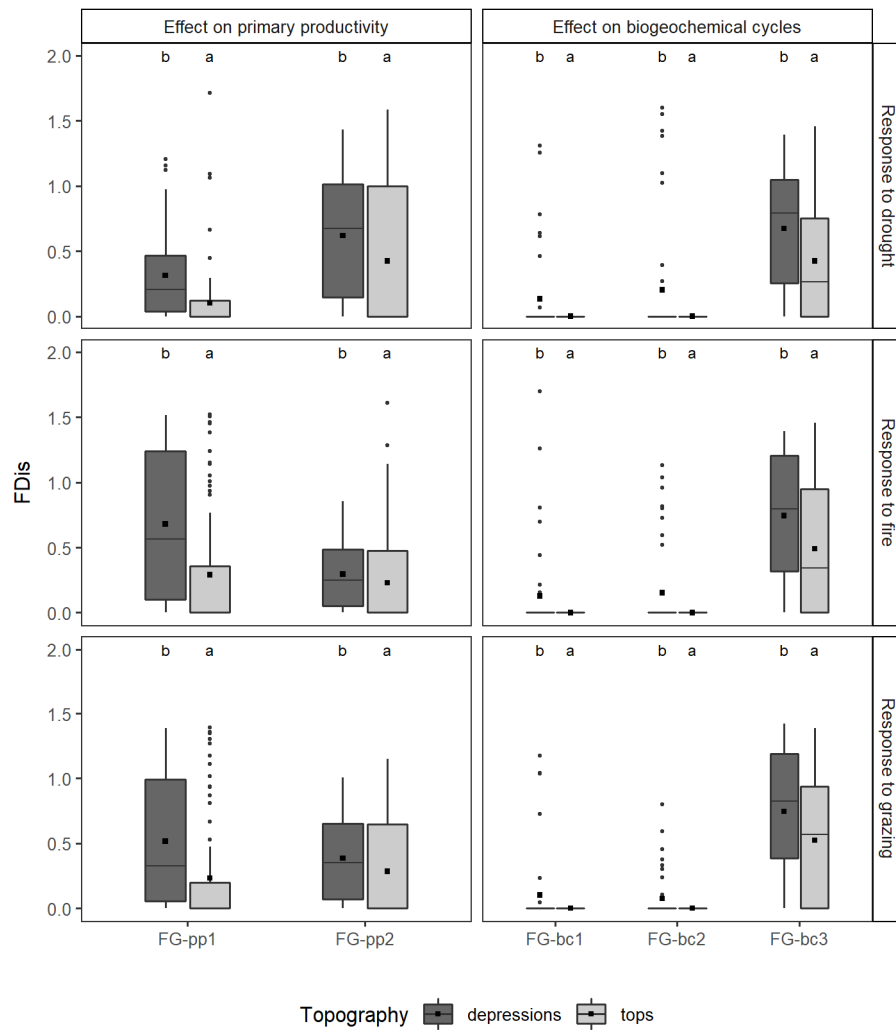


Figure 6.19 – Response diversity (to the three pressures) in each effect group for primary productivity and biogeochemical cycles, according to the topography ($n = 139$ plots). The means are represented by the squares. The letters indicate the differences between topographic elements according to the Wilcoxon's tests ($P < 0.05$).

6.4. Discussion

6.4.1. Influence of topography on current functional diversity

Current functional diversity has been studied through five indices (FRic, FEve, FDis, FDiv and CWM) calculated for each of the five sets of traits (three response sets and two effect sets) on the 139 plots inventoried in 2015. Mean comparisons have highlighted a significant effect of the topography on FD indices, though with contrasted differences according to the index. Functional richness, evaluated with the FRic index, is always significantly higher in depressions, except for the fire response set, for which the test revealed no significant differences even if the mean is slightly higher in depressions. This means that depressions host a larger panel of response strategies for grazing and drought than tops, and present more combinations of effects traits. Unlike the other indices, FRic is affected by species richness (Laliberté and Legendre, 2010; Villéger *et al.*, 2008). Indeed, having more species increases the chance to have extreme traits values and therefore increases the functional space. This result can thus partially be explained by the higher species richness in depressions.

Functional evenness (FEve) is always more elevated on tops, though with significant differences for grazing response and effect on primary productivity only. As the communities on tops present a lower density and a lower species richness, it can induce a higher regularity of traits values compared to highly diverse and denser communities, which are often located in depressions.

Functional dispersion (FDis) is similar on both topographic elements except for drought and fire response, which both present a higher FDis on tops. This indicates that species on tops present traits combinations further apart from the centroid of the functional space.

Finally, the CWM on the continuous traits and the FDiv show no difference according to the topographic position. Given the fact that we do have a difference in species composition according to the topography (see Chapter 4) and presenting different functional traits, the result of the CWM illustrates the fact that these species are rare and therefore have a limited effect on the CWM.

Interpreting and translating these results in terms of vegetation response and effect is difficult for two reasons. First, we are dealing here with multiple FD indices that do not present the same trends. For instance, a high FRic is not necessarily accompanied by a high FEve. Indeed, FRic, FEve and FDiv are

independent from each other (Villéger *et al.*, 2008). Mouchet *et al.* (2010) recommend using indices that reflect the three FD components (richness, evenness and divergence) to study the relationships between the environment, FD and ecosystem functioning as they bring complementary information. However, there are many studies that take one single index as a resilience proxy. For instance, Valencia *et al.* (2015) calculate FDis to measure the resistance of a Mediterranean ecosystem to aridity. Laliberté *et al.* (2010) and Craven *et al.* (2016) also rely on FDis to assess response diversity.

To our knowledge, the predicted form of the relationships between FD indices and response to pressures or effects on ecosystem functioning are not yet established (e.g. does a higher FEve/FDiv/FDiv assure a greater effect on ecosystem process or a better resistance to pressure?). It is the same for the relative importance of each FD indices. For instance, is it more important to have a higher FRic than a higher FDis in order to insure a maximization of different effects? For the effect traits, this might depend on the function considered. For instance, for a particular function of water infiltration, it might be more interesting to have a high FEve (i.e. species presenting all possibilities of root length) than a high FDiv (i.e. only species with very short and very long roots). An example of one of the few studies dealing with the link between FD indices and ecosystem functioning is the work of Le Bagousse-Pinguet *et al.* (2019). They point out a negative relationship between FDis and the N-C cycles and the ecosystem multifunctionality. For the response traits, we can assume that FDis might be more important than FEve in ecosystems with varied disturbances. Indeed, if traits distribution in the response-traits space is high, communities are more likely to resist to disturbances of large magnitude (compared to a community with lower FDis and greater FEve).

Topography does influence the FD of the three response strategies and the two sets of effect traits with at least one of the studied FD indices being significantly different: the results showed that depressions generally increase functional richness, just as it was the case for taxonomic diversity (Chapter 4). Communities in depressions thus present more traits values combinations than the communities on tops.

6.4.2. Changes in species pool, traits combination and FD

The distributions of traits values at the regional scale remained similar for the three periods for nearly all traits (section 6.2.5.1). We recall here that, while the division in periods follows the great drought, we do not assume that this drought is the underlying cause of the observed changes. The distributions for the fruit length, leafing period, leaf P content and seed weight presented a slight shift from the first to the second period. This could indicate either a shift in species composition between the first and the second period and a return to the initial composition during the third period; or the appearance of other species presenting similar trait values.

The analyses of traits combinations via Principal Coordinates Analyses revealed several interesting patterns regarding the link between species dynamics status (stable, decreasing, rare) and species response strategies. The PCoA on the set of drought response traits outlined that stable species present different traits values combination than the decreasing or rare species (Figure 6.7). As the drought pressure has known a major peak during the great drought, we can assume that this extreme event has influenced the species composition. The great drought, and possibly some minor drought events afterwards, have selected one strategy involving a long leafing period, relatively heavy seeds and a small vessel area. The only exception is the case of *Adansonia digitata*, which present different drought response than the other stable species. It raises the question of why *Adansonia* is still present and stable in frequency. It is possible that the population has been protecting it given its symbolic value and its edible fruits that are very prized. Its presence could therefore be “artificial” and not linked to its drought response strategy. Maranz (2009) observed such a pattern in the Sudanian parklands where population has maintained species with edible fruits.

The grazing pressure, which was hypothesized to have increased since the great drought, have had no influence on the trait values combinations. Indeed, stable and decreasing species do not seem to present a distinct strategy (Figure 6.9). It is the same for the fire response. We suggested four possible causes to explain why the traits combination for fire and grazing response have not changed. First, these two pressures might not have a direct filter effect on the species presence at this scale of analysis. Second, it is possible that some traits linked to those pressures have not been studied due to a lack of information for these traits. Third, demographic processes (such as recolonization after a disturbance) could

explain why a species is present or not. Fourth, random processes could influence the presence of a species.

At the community scale, we observed a significant loss of functional richness from 1970 to 2015 for the three sets of response traits (Figure 6.12). The changes are marked after the second period for the drought and grazing response whereas, for the fire response, the difference is already marked during the great drought. The lower functional richness indicates that the variety of responses for the three pressures is lower than before the great drought. We have seen that the decrease of mean FRic for drought response is likely to be due to the reduction of the FRic of the richest communities. As depressions host the richest communities in 2015, we assume that this was also the case in 1970. Therefore, we suggest that the decrease of FRic comes from a decline in functional richness inside depressions. As pastoralists have reported a decrease in species richness around temporary pond in the southern part of the sandy Ferlo (Herrmann *et al.*, 2020), it might support our hypothesis, as FRic is partially link to taxonomic diversity.

The loss of some response strategies could have consequences on the potential future woody communities and hence on the landscape. For instance, in the case of drought response, woody vegetation might not be able to respond to a change in the rainfall regime without any species migration. If mean annual rainfall would come to increase and that all species that were thriving under such environmental conditions are extinct, the ecosystem would not be able to return to a pre-drought specific composition. Besides, as the region south to the Ferlo has been largely transformed by agriculture these last decades (Tappan *et al.*, 2004) with a decrease in species diversity, it is unlikely that this area could be a source of more mesic species for a recolonization of the Ferlo.

For the sets of effect traits, the trend in FRic is different according to the function (Figure 6.13). On the one hand, functional richness for the primary productivity function showed a decline during the second period, followed by an increase. The means of FRic for the first and third period are therefore similar. On the other hand, FRic for the set of effect traits for the biogeochemical cycles presented a steady decrease from 1970 to 2015.

Having the same levels of FRic does not guarantee that the same effects are present. For instance, if we were to examine one single trait, the duration of leafing period, we might have a range of two months in the traits during two periods but with different species. Species with a leafing period of 2 to 4 months might be present during one period and species with a leafing period from 8 to

10 months during another. These two communities would still present a FRic of 2. Furthermore, the functional richness does not consider species abundances. Hence, the fact that dominant species have greater effect on ecosystem functioning compared to minor species might be overlooked (mass ratio hypothesis; Grime, 1998).

The community-level weighted means of trait values (CWM) also presented significant changes in means by period, from before to after the great drought, with the exception of fruit length. Some of the changes in the mean and/or in the interquartile range of four traits (decrease of maximum height, increase of leafing period, increase of wood density and decrease in vessel area) might be related to the consequences of the great drought, as these traits are linked to the drought response strategy.

The higher CWM of SLA is intriguing because a smaller SLA is usually associated with a higher allocation of tree resources in “leaf defense” (Cornelissen *et al.*, 2003). This increase may be due to the high SLA of *Acacia tortilis*, a species that has considerably increased in abundance since the great drought (see 5.3.3). *Acacia tortilis* is a drought tolerant species (in opposition to species presenting a drought avoidance strategy such as *Acacia senegal* and *Acacia seyal*) with a low hydric potential (Gebrekirstos *et al.*, 2008; Gebrekirstos *et al.*, 2006) that might allow it to tolerate a large SLA (a relative large leaf surface for a smaller dry weight).

The increase in mean leaf N content from before to after the drought (from 21.8 to 28.6 mg.g⁻¹) could also be due to the increase of *Acacia tortilis*, a N-fixer species, and of *Boscia senegalensis* (leaf N content of 28 and 34 mg.g⁻¹, Table 6.5). The decrease in leaf P content might be explain by a simultaneous relative increase of *Balanites*, *Boscia* and *Calotropis* which present low leaf P content (1.0, 1.5, 1.5 mg.g⁻¹ respectively; Table 6.5) and the decrease of species like *Acacia senegal* which has a high leaf P content (2.2 mg.g⁻¹, Table 6.5). Linking the changes in CWM to the species composition evolution is important. Indeed, some changes could be seen at first as beneficial for some additional services that were not studied in this research but a deeper analysis could reveal the opposite. For instance, the increase in mean leaf N content could be interpreted as good for livestock (we did not study an effect set of traits on fodder quality), though if it is due to an increase of *Boscia*, this species is not very appreciated by livestock.

The selection of species by pressure is not necessary driven trait by trait but rather by some combinations of traits values (i.e. species response strategies). So for traits like SLA, the observed changes in CWM may be a consequence of a

selection driven by other traits (i.e. there might be a compensation in the values of other traits). This is why we did not develop more physiological interpretations. The same is true for the potential direct interpretation of changes in CWM that some might want to link to additional effect sets (e.g. fodder quality), it is crucial to consider other compensatory features, such as palatability in the case of fodder quality.

One of the rare studies focusing on FD in semi-arid zones reported observations similar to our findings in dry forests of the Sudano-Guinean zone in West Africa (Aguirre-Gutiérrez *et al.*, 2020). They found a decrease in functional diversity (FDis) and an homogenization of communities these last three decades (Aguirre-Gutiérrez *et al.*, 2020).

6.4.3. Functional redundancy and response diversity

The study of the current vegetation functional redundancy allowed us to examine the potential ability of functional effect groups (created by hierarchical clustering) to persist through time, according to the insurance hypothesis (Yachi and Loreau, 1999). A high functional redundancy within a FG increases the probability of the FG of being maintained facing disturbances given that having more species implies a greater chance of having distinct responses.

In this work, functional redundancy is assessed by the number of species within each FG and is therefore independent of the response considered. We were able to look at the species repartition across groups. For the primary productivity function, functional redundancy is quite equilibrated between groups, without considering the topography. The FG-pp1 is composed of shrubs and bushes with a high leaf N content while FG-pp2 gathers mostly trees. Abundant species (see field inventory of 2015) are found in the two FG. The PCoA for the primary productivity function confirms this result as it showed that the stable species cover a large part of the functional space represented by the two first PCoA axes, meaning that the majority of the effect components are still maintained in the current landscape (Figure 6.10).

On the contrary, for the biogeochemical cycles function, species are not equally present between groups, as two FG out of three (FG-bc1 and FG-bc2) present a low functional redundancy. We can see on the PCoA for biogeochemical cycles that stable species are mainly gathered in one corner of the first two dimensions of the functional space (Figure 6.11). FG-bc1 gathers small deciduous species (e.g. *Grewia bicolor* and *Acacia senegal*), all rare or decreasing. FG-bc2 contains tall

deciduous trees like *Sclerocarya*, *Acacia seyal* and *Adansonia*, the only one stable species in this FG. FG-bc3 includes the most abundant species in the ecosystem of 2015 such as *Balanites*, *Boscia* and *Acacia tortilis*. These species are all evergreen and non N-fixer (except for *Acacia tortilis*). We assume that leaves of evergreen are tougher than the deciduous and potentially take a longer time to decompose. Besides, if these species do not shed their leaves every year, litter turnover is slower than for deciduous.

Topography influences functional redundancy as it was expected because of the higher functional richness of communities located inside depressions.

For a group to persist through time in a changing environment, response diversity is crucial, as it expresses the capacity of species within one functional effect group (and thus contributing to one effect on ecosystem) to respond differently to pressures. A high functional redundancy increases the probability to have a high response diversity but does not always insure it. Response diversity was assessed for the FG of the two sets of effect traits via the functional dispersion (FDis) within the response-trait space of three pressures (drought, grazing and fire).

Current response diversity presents the same patterns than the functional redundancy. FG-pp1 and FG-pp2 show a relatively high response diversity (FDis), potentially insuring higher resistance to the three studied pressures. On the opposite, for the biogeochemical cycles function, FG-bc1 and FG-bc2 present a response diversity close to zero for the three pressures, which means that these groups are more at risk of extinction facing these pressures.

From 1970 to 2015, functional redundancy of FG-pp1, FG-pp2 and FG-bc3, decreased during or after the drought then stabilized from 1972-1986 to 2015. However, mean functional redundancy of FG-bc1 and FG-bc2 continue to decline during the last two periods. This pattern is globally followed by the response diversity to the three pressures for the two effect sets, although the decrease in response diversity for fire is less marked.

The nearly complete disappearance of response diversity immediately after the great drought for the biogeochemical cycles function shows that the functional effect groups are in fact also functional response groups. The limit between effect and response traits is not always clear, as numerous traits can be classified in both categories (e.g. Lavorel *et al.*, 2011). An ACP on the coordinates of the first two dimensions of the PCoA on the three sets of response traits and the two sets of effect traits confirmed that the axes of the PCoA on drought response traits are

highly correlated to the two first axes of PCoA on biogeochemical cycles (results not shown).

If we assume that response diversity is tightly linked to the resilience (Elmqvist *et al.*, 2003), we can state that the resilience of all groups has eroded since the great drought. We assumed that drought and grazing pressures intensified through time though clear indicators of intensity were not available. This lack of information (e.g. estimates of livestock per decade) prevents a deeper analysis of the causes of the loss of resilience observed through response diversity analysis.

6.4.4. Strengths and limitations of the approach

The trait-based approach applied in this chapter presents several advantages to increase our understanding of ecosystem functioning and community dynamics compared to a classical taxonomic approach in which only species richness would have been studied.

First, functional diversity is directly linked to the influence of woody species on their environment via their effect traits. Response traits allow to apprehend the species dynamics and their persistence in the ecosystem which in turn will affect ecosystem functioning. Sterk *et al.* (2013) stated that response traits are related to the ecosystem resistance and effect traits to the recovery, which they identify as two properties of the resilience. The FD indices on sets of traits take account of the possible interactions between traits, without the necessity to know the nature of these relationships, through the computation of PCoA.

Second, the approach takes into account all the woody species and their abundances, whenever it was possible given the availability of field data. This allows to encompass the two types of effects that biodiversity has on ecosystem functioning: the mass ratio effects and the richness effects (Le Bagousse-Pinguet *et al.*, 2019). The mass ratio hypothesis states that the influence of a species on ecosystem functioning is directly proportional to its biomass (Grime, 1998), which suggests that the dominant species are the major drivers of ecosystem functioning. On the other hand, the richness effects are the consequences of the subordinate species.

Third, the utility of using species abundances was also outlined when comparing the results from the two spatial scales (landscape vs community). Indeed, according to the regional traits distribution at the regional scale (section 6.3.2.1) we still have the same range of traits inside the whole study area than before the

great drought. This situation is different at the community scale, as shown by the changes in CWM, which indicates that the local assemblages of species have changed.

Fourth, as traits data were gathered in the literature, the method is easily reproducible for other traits and species. The existence of standard protocols for traits measurements (Pérez-Harguindeguy *et al.*, 2013) also increases the reproducibility.

Finally, it is quicker and more global than an experimental approach in which indicators of functions would have been measured (for instance measure of soil nutrients content under and outside canopy to quantify the biogeochemical cycles). The relative speed of our approach compared to an empirical study has allowed to simultaneously study several responses and functions, which was interesting since the patterns in current and past FD were quite different according to the sets. While we do not question the importance of field experimental studies that remain crucial, the literature approach was well suited to our objective.

In addition to the inherent advantages of a trait-based approach, our methodology presents some originalities that reinforce its strength. First, researches often rely on one or two sets of traits (e.g. Chillo *et al.*, 2011; Laliberté *et al.*, 2010; Sterk *et al.*, 2013) and they don't always separate the pressures. For instance, Sterk *et al.* (2013) studied five response traits related to environmental variability but did not distinguish them. Here, three sets of response traits were analyzed. Second, we assessed FD using multiple FD indices, while studies sometimes focus on one single index (e.g. Craven *et al.*, 2016; Valencia *et al.*, 2015). This consolidated our conclusions.

However, the trait-based approach applied here, while showing an actual potential to better understand the ecosystem processes and how the organisms respond to pressure, suffers from several limitations. Some are due to a lack of knowledge in the domain (i.e. the uncertain relationships between the FD indices and the particular effects on the two studied functions or responses to the three pressures), while others are inherent to the adopted approach. We can group these limitations in three categories: traits values, inventory data (species abundances) and methodological choices.

The first category concerns the traits values and gathers three issues: missing values, intra-specific variations of traits and the reliability of the literature data.

The first issue is the missing values. Despite the selection of traits that are widely used in ecology, missing data are still frequent, particularly for species with a lesser interest at a global scale and/or for rare species. Indeed, functional trait databases mostly regroup measurements coming from projects that do not have the initial purpose to complete missing values in a database. For instance, species providing non-woody product (e.g. Arabic gum, fruits...) or useful wood are the most studied, like *Acacia senegal*. In addition, it seems like the Sahelian species are less studied compared to species from tropical forests. Information on hydraulic traits for instance are not available for many savanna species (O'Brien *et al.*, 2017). In some cases, traits data exist but are not published, which means that it can be difficult to obtain these data and if obtained, the methodology cannot be checked. Sankaran (2019) stated that the availability of data hinders our understanding of savanna drought response and therefore our capacity to draw future scenarios.

The second issue is that traits exhibit intra-specific variations, as stated in section 2.4.1. The attribute of a trait is assessed at the population scale for one time and place and may vary according to environmental gradient (phenotypic plasticity of traits; Mori *et al.*, 2013). The consequence is that the values collected among the literature might not be suited for the environmental conditions of our study area (the measures might have been taken on sites with very different environmental conditions). Variations of trait values can also occur according to the life stage (seedlings vs adults) and trait databases do not always mention on which stage the measure was taken (Aubin *et al.*, 2016).

The final issue of this first category is the reliability of the literature data. All the traits values have been collected among literature and/or databases. While the TRY database can be considered as a reliable source for traits values, it shows many missing data especially for our study area. Therefore, other sources have been consulted. Among these sources, the attributes for one species trait could vary, sometimes quite much. In addition, the range given by the source could be quite large. For instance, seed weight mass of *Acacia nilotica* varies from 87 mg (Garner and Witkowski, 1997) to 205 mg (Danthu *et al.*, 1996). It is likely that the protocols used to measure the traits differed from one source to another. Besides, in some cases, the methodology is not described and/or might not followed the methodology recommended by Pérez-Harguindeguy *et al.* (2013) for trait measurements. It is also possible that measurements were made in a different environment from our study area (see the previous issue about intra-specific variations). As the main focus of the present work was not on functional traits *per se*, we were not able to measure all the traits used in the approach.

The second category is the accuracy of the abundances data. As stated in section 3.3.2, Flotrop gathers a collection of different data sources using different methodology, sampling strategy and with an imprecise location. The integration of the Flotrop database in our analyses follows the assumption that the intensity of sampling is the same than the one from 2015. As the exact methodologies of Flotrop surveys are unknown, we are not in a position neither to confirm nor infirm this strong hypothesis that was necessary in order to have a glimpse at the temporal evolution of FD. Besides, species abundances are important to take into account in trait-based approaches as stated before.

The third category concerns the methodological choices we made (choice and number of traits, weighting, creation of functional groups).

The choice of the traits was dictated by their links with the studied pressures or effects, the availability of the data and their frequency of use in functional ecology (Weiher *et al.*, 1999). It has been showed that a relatively short list of traits are key determinants of plants response to environment or effect on ecosystem processes (Diaz *et al.*, 2004). Traits related to many functions are generally the most studied. For instance, in the TRY database, the number of entries was above 87 000 for the SLA, 158 000 for leaf size and 58 000 for leaf N content.

The second choice, though linked to the first, is the number of traits used to characterize response strategies and effects. Legras *et al.* (2019) stated that the number of traits (ranging between two to nine) could strongly influence the values of FD indices. Therefore, one must be careful while considering the exact values of FD indices. For instance, comparisons with other studies are not possible if the applied methodology is different. Yet, here we are interested by comparing values between topographic elements and between periods. The number of traits used by set ranges from six to 11. The lack of existing traits data is the main raison that prevented us of using more traits. On the other hand, the undesirable consequence of using too much traits is that some traits can bring redundant information. To avoid this inconvenient, we performed PCoA on traits before computing FD indices, as recommended by some authors (Laliberté and Legendre, 2010; Legras *et al.*, 2019; Villéger *et al.*, 2008).

The third choice we made was to disregard the potential relative importance of the traits within sets. Indeed, Gower's distance gives the same weight to each of the traits among one set, which might not be the case. For instance, a particular trait might be more linked to the function or the response studied than another. However, the information about traits relative importance does not exist to our

knowledge. Giving weighing to traits via expert knowledge would have brought subjectivity to the analyses, which we wanted to avoid.

Finally, our fourth methodological choice was the creation of functional effect groups. Functional classification of species is based on functional differences between species, which are continuous, so the categorization into groups has the consequence of losing some information (Villéger *et al.*, 2008). However, the computation of FG was, to our knowledge, necessary in order to assess the response diversity. There is also the subjectivity of the operator that influences the number of groups created. Here, because of the low specific diversity inherent of this arid zone, we kept the number of clusters as low as possible to insure that communities divided in clusters would still present species.

6.5. Conclusion

In this chapter, we undertook a trait-based approach of woody communities within our study area in order to enhance our understanding of the differences in species potential responses to drought, grazing and fire and the species effect on two ecosystem functions, primary productivity and biogeochemical cycles. We highlighted a decline in functional richness (FRic) for the three responses and for the effect on biogeochemical cycles from 1970 to 2015. FRic for the effect on primary productivity did present a fall during the drought which was followed by an increase from 1972-1986 to 2015. Changes in community-weighted means (CWM) were also observed, though traits distributions at the regional scale remained stable during the three periods. It can be tempting to directly interpret these changes in CWM in terms of response and/or effect but a trait-by-trait interpretation should be avoided, as compensatory factors may exist. Reasoning in terms of « species strategy » is more appropriate when it comes to analyze the species responses to disturbances. Further exploration could determine some typical “extreme” response strategies that would be characterized by a certain range of traits values (e.g. what would a perfectly drought tolerant species present as traits values for the set of response traits?) in order to have a “witness strategy” to compare the species between them.

We found that FRic of four sets of traits out of five was higher in depressions than on tops (FRic for the fire response being similar on the topographic elements). The influence of topography on FEve, FDiv, FDis and CWM was less marked. Functional redundancy and response diversity to the three disturbances were also always superior in depressions. Finally, we outlined that response

diversity for the five FG decreased since 1970, though in a lesser extent for FG-bc3, but with FG-bc1 and FG-bc2 presenting extremely low values (close to zero) in 2015.

Our analyses were carried out at two temporal scales (from before the great drought onward and in 2015) and at two spatial scales (regional/landscape vs local/community), which brought complementary information on FD. Considering multiple scales has outlined the importance of considering species abundances as stated by Mouillot *et al.* (2013). A special attention should be given in future field survey to record species abundances, preferably using a consistent methodology, and one that favors absolute counting rather than estimation.

As all of our traits data came from the literature (including TRY), we noted that many species (often minor species) still present missing data for some traits. We feel that traits measurement carried out in the frame of projects should be recorded in online databases such as TRY, which was consulted for this work and we encourage the open access to these kind of data. In addition, field measurement of traits including intraspecific variation could be quite interesting. Indeed, this aspect was not taken into account in our approach because of the lack of data. Still, if one species showed a high variability for some traits, it could represent as much functional variation than several species with low intraspecific variability. Besides, Aubin *et al.* (2016) stated that “intraspecific variation in traits is a direct expression of both genetic variation and the phenotypic plasticity of those traits”, two phenomena that are part of the species adaptive capacity mechanism that could allow species to persist in the short-term.

As enounced in section 6.4.1, the exact relationships between FD indices and ecosystem functions, (i.e. which indices are the most important for the occurrence of the processes) are currently lacking. For instance, while considering multiple complementary FD indices is important (Villéger *et al.*, 2008), the effect of combination such a high FRic, a low FDis and a high FDiv on ecosystem process is unknown. Are some indices more relevant to consider for particular ecosystem processes? To fill this gap of knowledge, we could directly measure some ecological functions on the field (e.g. primary productivity through the measurement of above- and below-ground biomass) and look at the relationship with FD indices of the field communities.

Finally, as the methodology is reproducible, further research could be made by focusing on other sets of effect traits more directly linked to ES provided by woody vegetation and that support pastoralism (e.g. a set of effect traits linked to the fodder quality). Some additional features (not “functional trait” *sensu stricto*)

such as tannin content or phenology of fruit production could be integrated and knowledge about these features could be improved.

We have listed a few potential limitations to our approach. Instead of discrediting the approach, it rather emphasizes knowledge gaps and helps to point some ways to improve trait-based approach. Finally, to our knowledge, it is one of the first research dealing with functional diversity of woody vegetation in the Sahel, though with this originality comes the downside of having no studies to compare directly our results.

Chapter 7

General discussion and conclusion

— *Outline* —

This chapter first aims at summarizing the key findings on the current state of woody vegetation and its spatial heterogeneity (Chapter 4); its long-term dynamics in terms of density, woody cover and species composition (Chapter 5); and the trait-based approach carried out on effect and response traits sets (Chapter 6). We then discuss the persistence of both woody vegetation and its effects on the two ecosystem functions studied (primary productivity and biogeochemical cycles) based on indicators derived from Chapter 4 to 6. We also give some insights about how persistence could be ensured and make suggestions for a potential management. Finally, we propose avenues for future research, based on the main challenges that we faced in this work.

7.1. Key findings

The main goal of this thesis was to evaluate the long-term trends (from 1965 to 2018) of woody vegetation in the Ferlo, the Sahelian sylvo-pastoral region of Senegal, in order to discuss the persistence of this vegetation and its effects on two ecosystem functions (primary productivity and biogeochemical cycles) regarding three disturbances (drought, fire and grazing).

Woody vegetation was studied at different spatiotemporal scales through different indicators (Figure 7.1). These were computed at different ecological levels: population (i.e. group of individuals belonging to the same species); community (i.e. local assemblages of species; e.g. an inventory plot in depression vs an inventory plot on hilltop); and landscape (i.e. the assemblage of communities within a region; e.g. the woody vegetation within our study area). Most of our analyses were conducted at two spatial scales, local vs regional (i.e. the study area), each of them linked to a level of “ecological organization”. The local scale corresponds to the level of communities, whereas the regional scale expresses the assemblage of communities at the landscape level. Several disciplinary angles were mobilized to achieve three specific objectives.

First, the current status of woody vegetation (specific objective 1) was studied through field survey at the local and regional spatial scale. The sampling of inventory plots was stratified according to the topography to account for the influence of water availability, which is determined by the interaction of rainfall amount, soil type and topography. We also account for a potential grazing gradient by locating plots at increasing distance from the deep wells (from 2 to 15 km). Overall, we inventoried 24 species in the adult stand, belonging to 15 families. The woody stand presents a density of 42.5 ind.ha⁻¹ and 37.1 ind.ha⁻¹ for adults and saplings respectively (weighted means for the study area according to the proportion of depressions vs tops). The mean woody cover is of 6.5%, reaching 25% in depressions and 5% on tops.

We did not detect a significant effect of the deep wells distance on the studied variables (specific richness of adults and saplings; densities of adults, saplings and seedlings; basal area; woody cover; and proportion of the eight most abundant species) at the studied scale. The only exception was for *Acacia tortilis* whose proportion in the woody stand increases, as we got closer to the deep wells.

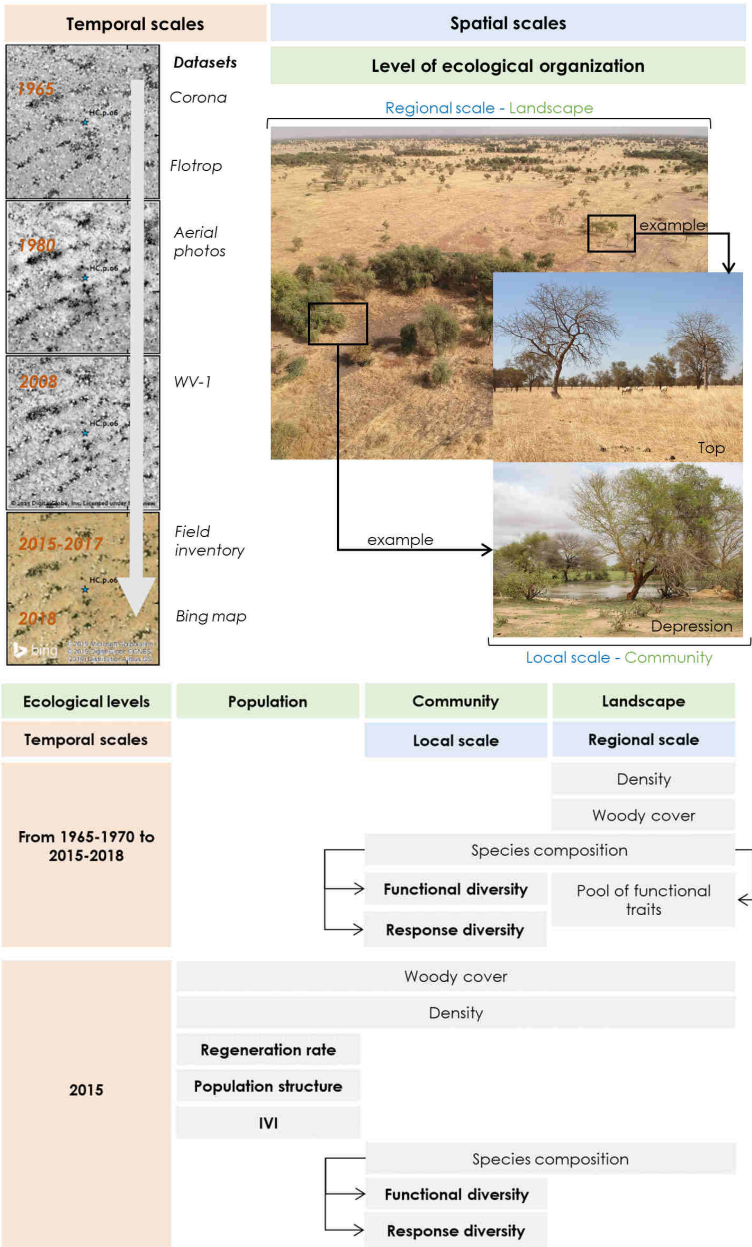


Figure 7.1 - Woody vegetation was studied at different temporal scales (from 1965 to 2018), spatial scales and levels of ecological organization (population, local communities and regional). The datasets used are linked to a period (except for traits dataset, which is not represented). Several indicators of woody vegetation state and temporal dynamics were assessed at these scales. In bold, “key” indicators used in the discussion about the persistence. Photographs from top to bottom: S. Taugourdeau (February 2019), M. Dendoncker (April 2015) and M. Dendoncker (August 2015).

While no significant influence of deep wells remoteness was found, woody vegetation does present a high degree of heterogeneity according to the topography with a higher density and a different specific composition (often more diverse) in depressions. The effect of soil type (or macrorelief) was not significant in determining the vegetation composition, specific richness and density, probably masked by the topography influence.

Woody vegetation is dominated by a few species at the adult phase on both topographic elements. The computation of the Importance Value Index, that takes account of species frequency, species dominance (in cover) and species relative density, reveals that *Balanites*, *Boscia* and *Calotropis* are the three first species in depressions and *Boscia*, *Balanites* and *Sclerocarya* the three first on tops. Secondary species include *Acacia tortilis* (5th position in depressions, 4th position on tops) and *Sclerocarya* (4th position in depressions). The other species are far behind and often present in the form of isolated individuals.

The population of seven species (*Acacia tortilis*, *Balanites*, *Sclerocarya* on tops and in depressions; *Acacia senegal* on tops; *Acacia seyal*, *Guiera* and *Grewia* in depressions) was analyzed through size class distribution. A large difference between the observed distribution and the negative exponential curve of a theoretical undisturbed population was observed for five of the species (*Acacia tortilis* in depressions, *Sclerocarya* on both topographic elements, *Acacia seyal*, *Guiera* and *Grewia*). On the opposite, the populations of *Acacia tortilis* and *Acacia senegal* on tops and *Balanites* on both topographic elements presented small differences with the theoretical curve (see PI analyses, Figure 4.4, section 4.3.1). In addition, the instability of population was outlined for all species except for *Balanites* (via the examination of mean quotient between classes and its standard deviation).

Overall, regeneration (seedlings and/or saplings) was found for 19 species, with, however, a great disparity among them. Saplings are dominated by a small number of species: *Balanites* and *Acacia tortilis* are the two tree species with the highest saplings densities (7.3 and 1.4 ind.ha⁻¹, weighted means for the study area according to the proportion of depressions vs tops). Yet, *Boscia* comes in first place if shrubs are taken into account, with 21.2 ind.ha⁻¹ and *Calotropis* occupies the third place with 6 ind.ha⁻¹. For 11 species (out of the 24 recorded at the adult stage), no saplings was recorded, despite the presence of seedlings for some of them. The spatial analysis of seedlings highlighted the importance of large trees to host regeneration, as 12 species out of the 16 present at the seedlings stage were located near relatively tall trees that offer a large cover (e.g. *Sclerocarya*).

The influence of topography and anthropogenic activities was outlined in other locations of the Sahel. For instance, Dembélé *et al.* (2006) indicate that vegetation structure and composition are mainly driven by water availability through the impact of topography and edaphic conditions (Mali, Sahelian zone). Local topography within our study area combines these two factors, as soils are slightly different between tops and depressions (in terms of depth, and clay and organic matter content). Poupon (1980), in the same zone as our study, observed that *Boscia* and *Guiera* were the two most abundant species on both topographic elements. Interestingly, he observes that *Balanites* has a low frequency inside depressions and represents less than 1% of the woody stand in these locations. On the contrary, within our study area, this species was recorded in 80% of the plots located in depressions and it represents 30% of the woody stand in terms of relative density. He also found that *Acacia senegal* was in low abundance and seems to favor depressions and their neighborhood, which is similar to our study where this species frequency is slightly higher in depressions (11%) than on tops (7%).

Dembélé *et al.* (2006) also stated that anthropogenic activities modify the spatial organization driven by water availability. On a gradient of human disturbances, they identify livestock grazing and fuel-wood collection as human activities that can induce changes in vegetation structure or increase in mortality rate for the collected species. They also observe a negative effect of wells proximity on the seedlings but not on the adults. Hejmanová *et al.* (2010) also identify these two activities as key determinants of woody vegetation structure. Yet, in our work, we did not found a significant effect of the deep well distance, at the studied scale.

The second specific objective was to study woody vegetation changes from 1965 onward using aerial photographs, satellite imagery, an historical vegetation database (Flotrop) and field inventories. Differences in the spatial scale studied often oppose botanists against remote sensing specialists and can lead to opposite observations about long-term trends (like the one in the debate “degradation vs recovery” of the Sahelian vegetation, Mbow *et al.*, 2015). By complementing aerial observations with field surveys, we were able to get to the level of species dynamics. Four indicators of changes were considered: density, woody cover, species frequencies and species assemblages. Density of large trees (bushes and shrubs were not visible on the oldest images) significantly decreased within the study area, from 14.8 ind.ha⁻¹ (1965), to 13.4 ind.ha⁻¹ (1980) to 11.9 ind.ha⁻¹ (2008), then stabilized in the last decade, reaching 12.2 ind.ha⁻¹ in 2018. Woody cover declined from 3.9% (1980) to 3.3% (2008). Slight differences

occurred according to location of the sites on dunes, plains or near Fulani camps, though not significant.

In addition, we detected a shift in community composition according to the Principal Coordinates Analysis that outlined a clear break between Flotrop records and recent inventories (2015-2017), with *Boscia*, *Calotropis* and *Leptadenia pyrotechnica* being more associated with current field surveys. This suggests a change of the ratio of shrubs vs. trees toward more shrubs. Finally, we analyzed the frequencies of the 40 species that were mentioned in the Flotrop database and/or recorded during our inventory. Only six species were classified as stable (*Adansonia*, *Balanites*, *Boscia*, *Calotropis*, *Leptadenia pyrotechnica*, *Ziziphus*), one was strongly increasing (*Acacia tortilis*) whereas 13 species were decreasing, among which *Acacia senegal*, *Acacia seyal*, *Combretum glutinosum*, *Grewia* and *Sclerocarya*. The rest of the species ($n = 20$) presented too few occurrences (< 5) to allow conclusions about their dynamics.

Changes in species composition and in the trees vs shrubs ratio have been outlined in other parts of Sahelian and Sudanian zone (Brandt *et al.*, 2014; Lykke, 1998). Similarly, our findings about density trends (a decrease followed by a stabilization or an increase) support the studies of Hiernaux *et al.* (2009) in Mali and of Zwarts *et al.* (2018) in south Mauritania and northern Senegal.

The third specific objective was to transpose the different indicators from the first two specific objectives at a functional level of the woody communities. For this purpose, we applied a response-effect trait-based approach on the field data (2015) and on the Flotrop database. We aggregated traits into three sets of response traits: drought, grazing and fire response; and two sets of effect traits, linked to two functions: primary productivity and biogeochemical cycles.

The study of temporal changes in traits pool shows that traits values have stayed similar from 1970 onward at the landscape level. However, at the community level, CWM have changed, indicating a shift in local assemblages of species. Functional richness has drastically decreased for the three response and for one of the effect set (biogeochemical cycles). FRic for primary productivity function has declined during the great drought but was followed by a slight recovery since then.

Hierarchical clustering based on effect traits created two functional groups (FG) for primary productivity and three FG for biogeochemical cycles. For primary productivity, FG-pp1 gathers shrubs and bushes with high leaf N content whereas FG-pp2 is composed of taller trees, both groups containing some

abundant and/or stable species. For biogeochemical cycles, FG-bc1 is formed by small deciduous species (all rare and/or decreasing species); FG-bc2 by taller deciduous species (all rare and/or decreasing species) and FG-bc3 by evergreen, often non-N fixer species (abundant and/or stable species).

Changes were visible in functional redundancy for functional effect groups of primary productivity and biogeochemical cycles. A loss of functional redundancy occurred in every FG during or after the great drought, either with a stabilization between the second and the third period (FG-pp1 and FG-bc3) or with a constant decrease until 2015 (FG-bc1 and FG-bc2). Response diversity to drought, fire and grazing of the different FG exhibits similar patterns than for redundancy, with more marked changes for drought response than for grazing and fire. The examination of current FD showed that depressions were hotspots for functional richness, though the other FD indices were often similar between tops and depressions. Functional redundancy and response diversity were also higher in depressions for the five functional effect groups.

While the results of our trait-based approach could not be compared to other studies (to our knowledge, they do not exist yet), the methodology is based on several research dealing with ecosystem resilience and ecosystem functioning (e.g. Chillo *et al.*, 2011; Laliberté *et al.*, 2010; Mori *et al.*, 2013; Mouillot *et al.*, 2011). Among the studies cited, three are field studies. Chillo *et al.* (2011) studied the response diversity to grazing of arid rangelands in Argentina based on six response traits. They focused on eight effect traits linked to nutrient cycling and soil retention. Laliberté *et al.* (2010) also studied response diversity using a meta-analysis with sites from five biomes, using 13 effect traits on biogeochemical processes and 12 response traits to disturbances (without distinguishing them). Mouillot *et al.* (2011) conducted a FD analysis of 26 plots located in European grasslands using five effect traits related to primary productivity and decomposition rate. The last study is a review (Mori *et al.*, 2013) that developed a conceptual framework to explain how the loss of response diversity could cause ecosystem degradation through a decrease of its resilience.

Beyond the specific objectives, two outputs emerge from this work and contribute to the originality of this work. The first output is the constitution of a solid and reliable geo-tagged field vegetation database in a region where field data are rare and/or lack of geolocalization and/or are derived from unknown methodology. The availability of vegetation field data is necessary to establish long term monitoring and/or to develop sustainable management strategies (Karlson and Ostwald, 2016). The second contribution is the amount of

literature/data gathered. A lot of literature about the vegetation of Sahel and Ferlo already exists. However, these valuable data are often unpublished. In this work, we wanted to take advantage of this grey literature and integrate it into our analysis.

7.2. Persistence indicators

7.2.1. Ecological situation

The final topic concerns the persistence of the woody vegetation within the study area, more precisely its ability to maintain the provision of ecosystem services supporting sylvo-pastoralism, in view of four observations. First, we outlined in Chapter 4 the current state of the vegetation with the dominance of a few species and the instability and the lack of regeneration of all other species population. Second, in Chapter 5, we highlighted a decrease in density and a shift in species composition that are occurring since 1965. Third, in Chapter 6, we showed a shift in CWM, a decrease in functional richness and in response diversity for the five sets of traits. Finally, the current pressures that are acting on this ecosystem, such as the population (human and animals) and the risk of intense drought are expected to increase in the future.

Discussing long-term trends of woody vegetation first requires characterizing the ecological situation we are dealing with. We may extrapolate, with caution, our findings to a larger spatial scale if the ecological situation is similar. To characterize the ecological situation, we adapted the checklist suggested by Grimm and Wissel (1997) and retained four items.

First, the ecological level (individual, population, community, ecosystem or landscape) and the variables of interest have to be defined. We focus on two ecological levels (Figure 7.1): the local level of woody plants communities (e.g. an inventory plot, local assemblages of species) and the landscape level constituted by assemblages of different communities present within the study area. Variables of interest are density, woody cover, species frequency, species composition, IVI, functional traits, functional diversity, response diversity, regeneration and population structure.

Second, the spatial and temporal scales have to be explicit. The spatial scale of reference is our study area, as defined in section 2.2.1. The maximal extent of the validity domain is the “sylvo-pastoral reserve of the six deep wells”, which implies that the land use is exclusively sylvo-pastoral. The period of interest extends from

1965 to 2015-2017-2018 (years of field inventories and of the last satellite images).

Third, the reference state, that is, what we consider as the “normal” state of the system, has to be described. As stated in the introduction (Chapter 1), the reference state is the one that allows the persistence of an extensive sylvo-pastoralism by delivering the ES that underpin this land use. To establish an exhaustive list of these ES and the ideal quantity and quality of provision is beyond our objective but we can still cite some key ES, described in 2.2.3: the provision of fodder, complementary food products, wood as fuel and material, maintenance of soil fertility, water regulation, nutrient cycling and microclimate (shadow for human and livestock).

Finally, the environmental pressures have to be listed. We studied three disturbances in our trait-based approach (drought, grazing and fire) but other pressures are active on woody vegetation: for example, among the anthropogenic pressures, direct uptake is also running along to grazing pressure; among the climatic pressures, the increase of temperatures was not taken into account either.

The great drought that struck the entire Sahel during the 1970s-1980s is considered as an extreme climatic event (ECE, Smith, 2011). Indeed, both the driver and the response were extreme. Precipitations decreased of 20 to 40% during 1970-1989 compared to the mean of 1901-1998 (Nicholson, 2001), which led to a drastic reduction of crop yields and widespread mortality of vegetation. In this work, we have field observations 30 years after the end of this ECE (though for some authors, drought continues during the 1990s, see section 2.1.2 and Figure 2.2). This will allow discussing the trajectory of woody vegetation since this ECE, in the frame of the climate change debate about impacts of ECE.

7.2.2. Persistence, ecological resilience and constancy

In this research, we are interested on the persistence of both woody vegetation and its effects on two ecosystem functions (primary productivity and biogeochemical cycles) while undergoing the pressures of drought, fire and grazing.

This topic can be related to the concepts of ecological resilience and constancy developed in Chapter 2 (2.3). While persistence is about “persistence through time of an ecological system” (Grimm and Wissel, 1997), ecological resilience focuses on how the system can persist under disturbances, without changing

functions (Brand and Jax, 2007; Holling, 1996); the functions being here the ones that underlie the provision of ES that support sylvo-pastoralism. Constancy means, “staying essentially unchanged” and its resistance aspect is defined as “staying essentially unchanged despite the presence of disturbances”.

Constancy implies that the systems can undergo some limited fluctuations while the persistence means that the system continues to exist as an “identifiable entity”. Applied to the study area, our interpretation of these two properties is that persistence can be viewed as the ecosystem staying a bush or tree savanna without crossing a threshold that would lead it to a degraded grassland or shrubland. These changes that might heavily transform the systems are similar to the “regime shifts” mentioned by Folke *et al.* (2004). Constancy and resistance are more related to whether the ecosystem still maintains the same functions even with minor changes in specific composition or density.

We did not study “resilience” as defined by Grimm and Wissel (1997) or the “engineering resilience” (Brand and Jax, 2007; Holling, 1996) which both focus on the recovery after a disturbance and the rate at which this recovery happens. Indeed, we did not compare the ecosystem before and after a disturbance (e.g. an experimental design to study communities within a fenced area, before introducing some cattle and then excluding them; to see how much time was required for the communities to reach their initial state). Instead, we studied the effect of the great drought but in an indirect way (no control experiment) and without disentangling the different drivers that were probably interacting (grazing, climate change, etc.).

One must be careful to differentiate *woody vegetation* ecological resilience from the *ecosystem* ecological resilience. While the former contributes to the latter, we did not study all the ecosystem components, such as herbaceous layer (and the effects that tree cover have on it; e.g. Grouzis and Akpo, 2006), animal and microbial communities. Relative importance of each component to the resilience is unknown, though we can safely assume that woody vegetation presence enhances other communities due to the creation of favorable habitats (e.g. Ochoa-Hueso *et al.*, 2018).

7.2.3. Variables and indicators

In practice, it is difficult to actually “measure” or quantify persistence, ecological resilience or constancy. Therefore, long-term dynamics of vegetation is assessed through several indicators. Some of the variables studied in Chapter 4, 5 and 6

are directly linked to the woody vegetation persistence and we will use them to discuss whether woody vegetation within the study area is likely to maintain the different facets (or effects) that are derived from the two functions studied here, primary productivity and biogeochemical cycles.

Four key indicators, derived from primary ecological variables are used to discuss the persistence: population structure, regeneration, functional diversity and response diversity (Figure 7.1). Indeed, we are looking to bring insights on the long-term dynamics of woody vegetation and to link this information to the functional effects (that insure the provision of ES) and responses (that determine the maintenance of species in the face of disturbances). Dendrometric variables on their own, such as density, do not provide such information. They are however important, as they serve to the construction of indicators more directly linked to the long-term trends and/or the potential future of vegetation.

Population structure is derived from the association of individual's circumference and their density. While it is a static image of the distribution of individuals between the circumferences classes, it is the results of recruitment and mortality events from many years and it provides useful information about the potential future of population as the regeneration capacity (saplings and individuals in the small classes) is assessed. The inconvenient of this indicator is that it could not be calculated for all the recorded species, as the analyses require a minimum number of individuals (fixed at 15 in this study). This means that we overlook minor species. As dominant species are thought to have a greater influence on ecosystem processes than minor (Walker *et al.*, 1999), population structure informs on the persistence of the effect of woody vegetation (abundant species) on the ecosystem processes.

Regeneration rate, on the contrary, is available for all the species. Saplings rate are more reliable than seedlings, as germination of seedlings might not be annual for some species (cohort phenomenon) and as saplings survival is more certain than seedlings. Functional diversity and response diversity come from the combination of traits data and species composition. These two indicators give information about all species, including minor ones, which may contribute significantly to the ecosystem resilience (Walker *et al.*, 1999).

The combination of these indicators can be particularly interesting. For instance, changes in response diversity, which links effect and response traits ("range of reactions to environmental change among species contributing to the same ecosystem function"; Elmqvist *et al.*, 2003), inform us about the persistence of the effect for the past decades. Combined with other variables or indicators that

give insight about the long-term trends (changes in species frequency and population structure), hypotheses can be made for the future of the effects.

7.2.4. Persistence of the studied functional effects

Assuming that the most abundant species have the most important effect on the ecosystem, we focus first on the species that present an Importance Value Index superior to 5%, separating tops and depressions (Table 7.1). We recall here that the IVI expresses the species ecological importance, as it is a composite indicator of relative density, relative frequency and relative dominance (based on crown cover) of species (see section 4.6). The IVI of one species is related to the values taken by the other species, as the sum of all IVI is equal to 100%. In the framework of a trait-based approach, and following the biomass hypothesis (Grime, 1998), we use it as a proxy for the amount of effect that a species has on ecosystem functioning.

For these species, we compare their belonging to the functional effect groups created (see 6.3.2.1), their dynamic status (according to the changes in frequencies from 1970 to 2015, see 5.3.3) and the main results from the population structure and regeneration analyses (see 4.3.1).

For the primary productivity function, we note that the repartition of the number of species between the two functional groups is equitable (both on tops and in depressions). As a reminder, FG-pp1 contains bushes and shrubs with a high leaf N content while FG-pp2 gathers only trees. That means that the effects of both FG are abundantly expressed in communities and, as there are stable species presenting a high regeneration rate, the future of the two FG is guaranteed.

The distribution of species among the FG for the biogeochemical cycles is more unbalanced. In communities on tops, four species among the five presenting an IVI above 5%, belong to FG-bc3 (evergreen or semi-evergreen non-fixer species mostly). *Sclerocarya* is the only representative of FG-bc2 (taller deciduous species). The effects of these two functional groups are therefore well expressed in the current landscape (on tops), given the relatively high IVI of the species. However, we note that FG-bc1 (small deciduous species) is not represented on tops. In communities located in depressions, FG-bc3 is well represented by four species and FG-bc2 by two species (*Sclerocarya* and *Acacia seyal*). Contrary to the tops, there is one species (*Grewia*) that belongs to FG-bc1.

As FG-bc3 is constituted by abundant, stable or increasing species with a high density of regeneration, the persistence of this group is assured, for both topographic elements. On tops, the persistence of FG-bc2 is likely at risk given the certain decline of *Sclerocarya*, identified as decreasing since 1970 and with no regeneration. In depressions, FG-bc2 could be maintained by the presence of *Acacia seyal* if *Sclerocarya* came to disappear. Indeed, *Acacia seyal*, while having an unstable population, still presents saplings to insure the renewal of its population. However, the persistence of the effect for FG-bc1 is threatened, as *Grewia* is decreasing and has a low regeneration rate (Table 7.1).

What would happen if these currently abundant species ($IVI > 5\%$) came to disappear? Could minor species insure the persistence of FG-bc1 and FG-bc2? If we look at the response diversity to the three disturbances for these two groups, we recall that it was extremely low on tops (zero for both groups for the three responses). In depressions, the values stay low, though significantly higher than for tops.

Even if Walker *et al.* (1999) stated that « there is no *a priori* definition of ideal level of diversity and/or redundancy in ecosystems », we assume that a response diversity close to zero is not ideal. Besides, we are more interested in the relative values of tops vs depressions than in the absolute values. That means that FG-bc2 on tops could be in critical danger in case of an increase of drought pressure, grazing or fire, given their low response diversity (and in case of the disappearance of *Sclerocarya*). It might also be the case of FG-bc1 in depressions (under the same conditions: disappearance of *Grewia* and/or increase of the three pressures). Depressions, in addition of presenting an additional abundant species for FG-bc2, and thus potentially insuring a stronger expression of the effect of FG-bc2, present a higher response diversity than the tops, which could secure the persistence of this group and of FG-bc1, not present on tops.

What remains uncertain is at which pressure intensity the currently abundant species from FG-bc1 and FG-bc2 (*Grewia*, *Sclerocarya* and perhaps *Acacia seyal*) might disappear and/or the time horizon for that shift to occur. As large old trees are vulnerable to drought (Lindenmayer and Laurance, 2017) and as global warming will increase drought impacts on trees through temperatures rise (Choat *et al.*, 2018), the time window during which we could act might be narrow.

The two studied functions are linked to several ES (provisioning services, carbon sequestration, and soil fertility). Maintaining the diversity of effects on the long-term could therefore contribute to the continuation of these ES, under the assumption that having a high diversity of effects enhances the provision of ES.

Table 7.1 – Key indicators of the dominant species (IVI > 5%) and minor species (1% < IVI < 5%) on tops and in depressions. Species density comes from the field inventory of 2015 (section 4.3.1). The columns “FG-pp” and “FG-bc” indicate the functional effect group of the primary productivity and the biogeochemical cycles functions respectively. The population and regeneration column summarizes the main results from the population structure and regeneration analyses (sections 4.2.3.2 and 4.2.3.3). Dynamic status highlights the species trajectory from 1970 to 2015 (section 5.3.3, S: stable, D: decreasing, I: increasing, R: rare). Species acronyms (by alphabetical order): ACN: *Acacia nilotica*, ACT: *Acacia tortilis*, ADD: *Adansonia digitata*, ASN: *Acacia senegal*, ASY: *Acacia seyal*, BOS: *Boscia senegalensis*, BAA: *Balanites aegyptiaca*, CAP: *Calotropis procera*, COG: *Combretum glutinosum*, GRB: *Grewia bicolor*, GUS: *Guiera senegalensis*, LEP: *Leptadenia pyrotechnica*, SCB: *Sclerocarya birrea*, ZIM: *Ziziphus mauritiana*. The stars indicate the species only found in depressions.

Tops						
Sp	IVI (%)	Density (ind.ha ⁻¹)	FG-pp	FG-bc	Population and regeneration	Dynamic status
Dominant species (IVI > 5%)						
BOS	30.7	18.4	1	3	Structure not analyzed but plenty of saplings	S
BAA	23.3	6.9	2	3	Numerous seedlings and saplings; stable population	S
SCB	19.2	2.7	2	2	No saplings, unstable population	D
ACT	7.5	1.6	2	3	Numerous seedlings and saplings, stable population	I
CAP	6.5	3.1	1	3	Structure not analyzed but plenty of saplings	S
Minor species (1% < IVI < 5%)						
COG	3.4	0.5	2	3	No regeneration	D
ASN	2.6	0.6	1	1	Regeneration present, unstable population	D
ADD	2.3	0.2	2	2	No saplings	S
GRB	1.4	0.2	1	1	No saplings	D
LEP	1.1	0.3	1	3	Regeneration present	S
GUS	1.1	0.3	1	3	Regeneration present, unstable population	D

Table 7.1 – continued.

Sp	IVI (%)	Density (ind.ha ⁻¹)	Depressions		Population and regeneration	Dynamic status
			FG-pp	FG-bc		
Dominant species (IVI > 5%)						
BAA	29.6	48.4	2	3	Numerous seedlings and saplings, stable population	S
BOS	22.7	66.6	1	3	Structure not analyzed but plenty of saplings	S
CAP	8.9	23.3	1	3	Structure not analyzed but plenty of saplings	S
SCB	8.8	3.5	2	2	No regeneration, unstable population	D
ACT	6.2	2.8	2	3	Numerous seedlings and saplings, stable population	I
GRB	5.6	4.2	1	1	Low regeneration, unstable population	D
ASY*	5.0	3.9	2	2	Regeneration present, unstable population	D↓
Minor species (1% < IVI < 5%)						
GUS	2.1	1.7	1	3	Regeneration present	D
ZIM*	2.0	0.9	2	3	Low regeneration	S
ACN	1.5	0.4	2	2	No saplings	R ¹⁷
COG	1.5	0.7	2	3	No regeneration	D
ASN	1.5	0.5	1	1	Regeneration present	D

7.2.5. How to ensure persistence?

These considerations bring us to identify three species (*Acacia seyal*, *Grewia bicolor*, *Sclerocarya birrea*) that are currently abundant within the study area, as target for some kind of protection in order to insure the persistence of the effects provided by two of the three functional groups for the biogeochemical cycles function (FG-bc1 and FG-bc2).

From 1970 to 2015, response diversity to drought, fire and grazing for biogeochemical cycles has decreased in nearly all FG. It is likely to continue to decrease in the near future due to the lack of regeneration of some currently

¹⁷ Classified as rare because it was not recorded in Flotrop and it was therefore not possible to establish its trajectory.

relatively well-represented species (e.g. *Sclerocarya birrea*) and some other minor species.

Therefore, in addition of these four species, we might suggest minor species (though not rare) that could also benefit to be protected in order to maintain, if not response diversity, at least functional redundancy within FG-bc1 and FG-bc2 for biogeochemical cycles. We identify minor species as species with an IVI above 1%. We assume that values under 1% translate a negligible effect on ecosystem functioning.

Under this definition, we identify six minor species on tops and five in depressions (Table 7.1). Among them, we target those belonging to FG-bc1 and FG-bc2, as we established that the persistence of FG-bc3 was guaranteed, if the current environmental conditions (low rainfall and increase of temperatures) remain constant in the future. On tops, *Adansonia digitata* could be protected for insurance of FG-bc2. In addition, the presence of *Acacia senegal* and *Grewia bicolor* could be enhanced in the purpose of expressing the effect of FG-bc1, currently lacking on tops. In depressions, *Acacia nilotica* and *Acacia senegal* are potential targets as well, for the persistence of FG-bc2 and FG-bc1 respectively.

Of course, these suggestions are relevant only if our functional classification is considered as valid. Yet, even if this classification might be questioned, the approach of targeting particular “key” species in order to increase the probability of persistence of functional groups could be reproduced.

In addition to the identification of species to protect in order to enhance communities functional redundancy, the particular role of depressions has to be outlined, as several facts point out that these sites might be important for the resilience of woody communities at the landscape scale.

In Chapter 4, we identified topography as a determinant factor for the differentiation of woody vegetation in terms of density (of adults and regeneration) species richness and species composition. This effect has been confirmed at the functional level.

On a temporal dynamic perspective, changes in density, woody cover, species composition and frequency were assessed at the landscape level (Chapter 5), with no distinction of the topographic elements due to a lack of information. We are therefore not in position to establish whether the extent of the observed changes were different according to the topography. It is similar at the functional level, whose changes were evaluated at the same level (landscape).

Yet, the current response diversity to drought, grazing and fire is significantly higher in communities located in depressions than in communities on tops for every functional group of the two studied functions. FRic for the three sets of response traits is also significantly higher in depressions (with the exception of fire response, for which the difference was not significant). That means that, even if our functional classification was contested, the probability for having higher response diversity in depressions remains high.

The low regeneration for many species and the past long-term trend for response diversity suggest that response diversity could continue to decrease in the near future. The timing for this predicted decrease is unknown. If the current communities persist for several years, we already identified some species that could benefit from protection.

In addition, depressions might be a refuge for some species and act like a pool of taxonomic and functional richness for the re-colonization of tops, at least for species that are common of both topographic elements, like *Adansonia* or *Sclerocarya*. The installation of some semi-protected area in depressions, where the drought pressure is lower, might help to regenerate the adult population if we could protect seedlings from livestock. We suggest that these protected zones should not systematically cover all the area belonging to one depression, as these sites are frequently used by livestock for its shade and/or for the temporary ponds that are formed in interdunal depressions.

The importance of depressions can be further outlined.

First, depressions can be assimilated to “fertility islands”. In drylands, fertility islands correspond to areas of nutrient-rich soil, with relatively dense woody cover compared to the surroundings (Schlesinger and Pilmanis, 1998). Such areas are often the consequences of slope and soil texture and have been identified as a key determinant for ecosystem functioning (Ochoa-Hueso *et al.*, 2018; Whitford and Wade, 2002). Indeed, they have the potential to present a high degree of multifunctionality. Based on field data from drylands on the five continents, Ochoa-Hueso *et al.* (2018) have found that the most fertile islands (i.e. those presenting the higher number of soil functions; measured by indicators of C, N and P cycling) are located in sites with lower elevation. In our study, we found that FG-bc1 is only expressed in depressions (based on dominant species), potentially translating a higher multifunctionality (though trade-offs between effect groups can exist).

In addition, Ochoa-Hueso *et al.* (2018) showed that functional traits of woody communities influence the formation of such places, with a positive effect on multifunctionality of tall tree species combined with low-SLA values, probably due to a lower decomposition of litter and a subsequent accumulation of organic matter, which in turn favors an important microbial activity. Within our study area, *Adansonia*, *Sclerocarya*, *Combretum* and *Balanites* in a lesser extent are species that could favor the creation of fertility islands due to their elevated height and their low SLA.

Second, Berdugo *et al.* (2020) showed that response of multiple ecosystem attributes (physical, biological and chemical; e.g. plant cover, soil organic carbon) to an increase of aridity is not linear, which implies the existence of thresholds. They further found evidence that suggests an interaction between aridity and other environmental factors, such as topography or land use, in the determination of these thresholds. Therefore, they suggest that actions on these factors might offer some possibility to mitigate these abrupt changes. As aridity is forecasted to increase in the future, the role of depressions might be exacerbated.

Future research could focus on depressions and their potential heterogeneity (e.g. depressions in dunes vs depressions forming temporary ponds in plains), which has not been studied here. Particularly the study of depressions size, soil hydric properties, and functional attributes of communities might highlight which depression types enhance multifunctionality and/or response diversity. This suggestion might be reinforced by the “scarcity” of depressions in the landscape, as they cover approximately 6% of the study area (section 4.2.2). Finally, studying landscape connectivity could help understanding how depressions are connected and how this diversity could travel through landscape (Craven *et al.*, 2016). Indeed it has been suggested that such network could play a key role in restoring response diversity (Bengtsson *et al.*, 2003). Such an analysis should take into account, as far as possible, the role of livestock in connecting these depressions. Indeed, cattle, sheep and goats intervene in the network as dispersal agents for some woody species, as livestock rests in the shade of tall trees, eats fruits and is susceptible to drop seeds under other trees several km away. The connectivity analysis will be realized in the frame of the CASSECS project, which was launched in 2020.

Moreover, the spatial vegetation patterns might have evolved through time, from a diffuse vegetation to a more spotted texture (Barbier *et al.*, 2006; Kusserow, 2017). Though we have not studied this aspect, we can observe a slight change

in this pattern on the series of aerial photos and WorldView-1 images (Figure 5.4). Therefore, it might be interesting to include the temporal dynamics of such networks in a connectivity analysis.

Finally, almost all rare species (with one or two individuals recorded in 2015) were inventoried only in depressions: *Acacia ataxacantha*, *Adenium obesum*, *Anogeissus leiocarpa*, *Bauhinia rufescens*, *Combretum aculeatum*, *Dalbergia melanoxydon*, *Feretia apodanthera* and *Stereospermum kunthianum*. The exception are *Commiphora africana* and *Faidherbia albida*, which were also recorded on tops.

We discussed the role of abundant species as predominant for the current effects on ecosystem and minor species as “backup” species. What is, however, the role of rare species in the ecosystem? Due to their scarcity, it is unlikely that their effects on ecosystem functioning are large (biomass hypothesis; Grime, 1998). Besides, their extremely low population size prevent them of the capacity to replace dominant or minor species in case of disappearance of one of them.

Yet, their likely marginal effect on the two studied functions does not mean that they are unimportant. Rare species are indicators of a loss of biodiversity, as they are most likely reflecting past environmental conditions during which they could have been more abundant (minor or dominant). The life span of Sahelian species is currently not well known but in case of long-lived species, their population may persist during long period even if the recruitment is no longer active (Eriksson, 1996). As we detected 48% of unchanged trees between 1980 and 2008 (see section 5.3.2.2.), it is a first indication that some individuals/species can live at least 30 years (as they had to be sufficiently tall in 1980 to be seen on aerial photos). In addition, some individual trees inventoried on the field ($n = 91$) have also be localized on aerial photos, providing some further information at the species level (see Appendix 26).

The importance of rare species lies in their potential capacity of creating habitat for other species (e.g. birds; see Zwarts *et al.*, 2018); their use in traditional pharmacopoeia or their cultural uses by local population. Either ways, these benefits cannot be captured by a trait-based approach on the two studied functions.

To better understand the importance of rare species for local population, ethnobotanical surveys could be integrated to future research. Moreover, while our inventory did cover the principal source of variation of the vegetation, we still observed several species on the field that were not within our plots (see Appendix 21). In this regard, interviews could help tracking these rare species

(Lykke *et al.*, 2004) and assessing vegetation changes (Lykke *et al.*, 1999; Sulieman *et al.*, 2012; Wezel and Lykke, 2006), bringing complementary information to field inventory. The participation of local land users could also help to identify indicators of the vegetation state that are the most relevant for them and easily measurable on the field in order to carry out widespread vegetation monitoring (Herrmann *et al.*, 2020).

7.3. Vegetation long-term dynamics after an extreme climatic event

The study of long-term trends of density and woody cover in Chapter 5 highlighted a decrease of these indicators from 1965 to 2008 followed by a slight recovery (density). Based only on remote sensing indicators, we could have interpreted this increase in woody vegetation density as a good sign for the provision of ES (assuming that a higher tree cover insures a higher level of ES). However, we detected a shift in species composition and frequency along with changes in functional diversity and potentially in the ES supported by the two studied functions. Indeed, some species representing two functional effect groups (FG-bc1 and FG-bc2) and still abundant in the current ecosystem, have been identified as decreasing, by the analysis of their changes in frequency (past decrease) and by their population structure (forecasted decrease).

Our analysis has been separated in three periods according to the great drought, considered as an extreme climatic event (ECE). In the future, the frequency of ECE is predicted to be rising, due to the climatic variability and the increase of temperatures (Lloret *et al.*, 2012), the latter already occurring in our study area since the great drought, as shown by Figure 3.5 (increase of the minimum annual temperatures). The length of our data series makes it possible to discuss the long-term impacts of an ECE, with our recent field inventories carried out 30 years after the extreme event (if we assume that the year 1984 marks the end of the great drought).

While ECE can sometimes, but not always, trigger vegetation shifts, there is still few evidence of such events (Lloret *et al.*, 2012). We argued that the changes observed at the studied temporal scale is one evidence of an occurrence of a vegetation shift. Vegetation shifts can be related to the extremeness of ecosystem response as described by Smith (2011), as being one of the condition to qualify an event as ECE. She stated that the ecosystem response should include “the re-ordering of key or common species in the community, widespread species loss

and/or invasion of novel species, with subsequent large and potentially persistent effects on ecosystem structure and function” (Smith, 2011). These changes thus occur at a higher ecological level than the population (e.g. an increase in mortality rates for some species).

In the first years of the great drought, Bille and Poupon studied the impact of the year 1972 (one of the first in severe deficit) on the population of the six most abundant species in Fété-Olé (Figure 2.4). They observed mortality rates ranging from 0.2% (*Boscia senegalensis*) to more than 50% (*Acacia senegal* and *Guiera senegalensis*; Poupon, 1980; Poupon and Bille, 1974).

In our study, we worked at a long-term scale and included all the species (at least the ones recorded in Flotrop and in our inventory). We confirm that the mortality observed during the next years after the drought was in fact followed by: (i) a loss of species (decrease in species richness); (ii) changes in species composition of communities and (iii) changes in FD (CWM) that potentially affected ecosystem processes. These three observations thus meet the “ecosystem response threshold” criterion of Smith (2011).

The woody vegetation within our study area, while conserving its identity as an open savanna (the persistence property, see section 7.2.2), did present a shift in the vegetation composition and structure from 1965 to 2018. Moreover, while the identified FG are still represented in the current woody vegetation, some of them could disappear in the near future, as showed in 7.3.4. Therefore, if the constancy and resistance properties can be considered as fulfilled from 1965 to 2018, woody vegetation is probably on the verge of a state from which it will not show these properties anymore.

We must keep in mind, that, while the great drought is likely the most extreme disturbance that the system has known since 1965, other pressures (anthropogenic) have added to the effect of drought and it is challenging to disentangle the relative effects of these factors. We are therefore not in position to attribute all the observed changes to the great drought.

Finally, as the years from 1935 to 1965 were very wet (above normal, see SPI, Figure 3.7), the vegetation before the great drought had probably reached its maximum woody cover (Bremen and Kessler, 1995) and most likely its maximum taxonomic and functional richness, as seen in the FD analysis. Therefore, the vegetation that faced the great drought was able to persist as open shrubby/tree savanna due to the presence of drought resistant species such as *Balanites*, *Boscia* and *Acacia tortilis*. Given the currently low response diversity to the three studied

pressures for the two studied functions, the current vegetation could be less able to resist to a second ECE or to a combination of increase pressure of grazing, fire and drought.

7.4. Perspective for future research

In the former section, we already suggested two leads for future research: focusing on depressions features (soil hydric properties for instance), their spatial organization and landscape connectivity; and integrate local knowledge to vegetation assessment. Here, we propose some additional possible avenues that could respond to the challenges encountered in the present work.

This study has strengthened the interest of multidisciplinary approach to study long-term trends of woody vegetation and its resilience, as it was outlined by several authors of different disciplines (e.g. Aubin *et al.*, 2016; Brandt *et al.*, 2015; Herrmann and Tappan, 2013). It also presents the advantage of dealing with a relatively long-term scale, as the most ancient data are from 1965. Long-term observations are crucial to understand the consequences of recurrent droughts and to detect potential ecosystem shifts (Epule *et al.*, 2014).

One of the main obstacles common to many of our analyzes was the existence and/or the availability of data. First, we noticed the lack of knowledge on the regeneration of Sahelian species and on soil seed banks. Yet, regeneration is an important feature of the population dynamics as it informs on the persistence of the current population. In our study, we did not systematically distinguish the origin of the regeneration (seedlings sprouts, root sucker or coppice). It would be interesting to record this information during field inventory, as species persistence via adaptive capacity is the result of two phenomenon, phenotypic plasticity and genetic capacity (Aubin *et al.*, 2016). If seeds regeneration is less abundant than clonal regeneration (which is most likely the case for *Balanites*, according to our field observations), genetic diversity could decrease.

Second, the study of the temporal dynamics was hindered by two factors. On the one hand, we struggled to obtain historical aerial photographs, though they proved themselves as a precious source of information of the vegetation density and woody cover during the great drought. We encourage the digitalization and open access of such data.

On the other hand, we noticed the absence of available geotagged old field surveys, which prevent us to study the changes of species composition on the

same sites. While Flotrop was extremely useful to study changes at the landscape scale, the localization was not precise enough to allow to conduct an inventory on the same sites. Besides, between 1986 and 2015, no field data were available, though our study area is a frequently studied zone of the Ferlo. We recommend that vegetation field data should be published, with an easy access of at least their localization and methodology of collection. The localization of our field plots will be available as part of our second paper, in Regional Environmental Change¹⁸. As a result, a network of historical inventory plots could be available for future studies.

Third, the trait-based approach revealed many missing trait data for Sahelian species. While the gathering of traits via literature was essential for our objective, future research on traits should include the measurement of some key traits on Sahelian species, and account for intra-specific variability. Indeed, the lack of data for drought-survival traits alters our capacity to understand savannas drought responses (Sankaran, 2019).

In particular, we identify two traits that are ecologically important and currently suffer from a lack of knowledge. First, the SLA, as it is tightly linked to plant ecological strategies (Westoby *et al.*, 2002). Second, the rooting depth, both on tops, where soils are deeper and in depressions, as it is unknown for all the species encountered in our study area. The only proxy for belowground traits used in this study was the presence of a taproot, and it still presents many missing data.

It has been stated that drylands have received less interest than other biomes such as humid tropical forest, because drylands have often been seen as areas with poor resources (Siyum, 2020). Yet, tropical savannas, the vegetation type studied in this research, are threatened by anthropogenic activities and the forecasted increase of intense and frequent droughts (Sankaran, 2019). It is therefore crucial to understand their long-term dynamics, and their response to drought or other disturbances in order to identify factors that might contribute to maintain the ES provided to the 270 millions of inhabitants of African drylands (White and Naeem, 2003).

¹⁸ Accepted with minor modifications at the date of July 12 2020.

7.5. Conclusion

The main key findings of this research can be summarized as followed:

- Local topography plays a major role in determining the woody vegetation richness (taxonomic and functional), composition, density (adults and regeneration) and response diversity.
- Long-term changes in species composition and in the trees vs shrubs ratio along with the current lack of regeneration for most tree species are three indicators of a potential transition from a tree savanna to a shrub savanna.
- The functional approach revealed a change in CWM of maximum height, leafing period, SLA, leaf area, seed weight, wood density, vessel area, leaf N and P content. For some traits (leafing period, wood density, and vessel area), we detected an homogenization between communities.
- A decline in response diversity to the three pressures (drought, fire, grazing), was outlined for most of the functional effect groups on primary productivity and biogeochemical cycles from before to after the great drought. All functional groups are currently represented in the ecosystem with relatively abundant species, but their future is endangered due to, among others, the lack of regeneration of many species.
- Depressions could be the key elements to a sustainable management of these ecosystems (or to maintain the persistence of woody vegetation and its effects on ecosystem functioning). The originality of our analysis lies on the analysis of woody vegetation at the species level and on the traits-based approach, which is, to our knowledge, one of the first study of this kind in the Sahel.
- The functional diversity methodology can be easily expanded to other sets of traits (e.g. effect on fodder quality) and/or to other systems.

Appendices

Appendices to Chapter 2	225
Appendix 1 : List of species, abbreviations, family and Fulani names.....	226
Appendix 2 : Illustrations of the study area.....	228
Appendix 3 : Multivariate analyses used in this work	233
Appendix 4 : Formulas of functional diversity indices	236
Appendices to Chapter 3	239
Appendix 5 : Landscape physiognomy.....	240
Appendix 6 : Vegetation types inside the study area.....	242
Appendix 7 : Soils, topography and water content	246
Appendix 8 : Climatic indicators	248
Appendix 9 : Fulani camps recording.....	250
Appendix 10 : Metadata on the inventoried plots in 2015-2017.....	252
Appendix 11 : List of some GIS data collected.....	257
Appendix 12 : Species list researched for traits values.....	259
Appendix 13 : Sources for response and effect traits	261
Appendix 14 : Sources consulted for traits data compilation.....	264
Appendices to Chapter 4	267
Appendix 15 : Species inventoried at the adult stage in 2015.....	268
Appendix 16 : Features of the nearest adults from seedlings	269
Appendices to Chapter 5	271
Appendix 17 : Results of the linear mixed models	272
Appendix 18 : Validation of the classification with 100 points per site.....	273
Appendix 19 : Evolution of woody cover on the 17 sites of 1 km ²	274
Appendix 20 : Species inventoried in 2017.....	283
Appendix 21 : Species composition per climatic period.....	285
Appendices to Chapter 6	287
Appendix 22 : The dissimilarity function.....	288
Appendix 23 : Principal component analysis on species traits	289
Appendix 24 : Temporal changes in functional diversity.....	291
Appendix 25 : Functional diversity in 2015.....	293
Appendices to Chapter 7	297
Appendix 26 : Trees present since 1980 within the study area.....	298

Appendices to Chapter 2

Appendix 1: List of species, abbreviations, family and Fulani names

This list gathers all the species mentioned in this document. Therefore, some of them were not inventoried on the field nor recorded in the Flotrop database. The classification (species names and families) refers to Arbonnier (2019) who follows the classifications APG III and IV (Angiosperm Phylogeny Group). Two species have had their names changed in the new classification APG. I mention both their previous and new names.

Table A1.1 – Woody species mentioned in the document. “Abbr.” indicates the species abbreviation in three letters. The Fulani names come from Fotius *et al.* (1967) and have been adapted according to my field experience.

Species	Abbr.	Family	Fulani names
<i>Acacia ataxacantha</i> DC.	ACA	Fabaceae	Goutouti
<i>Acacia erythrocalyx</i> Brenan	ACE	Fabaceae	
<i>Acacia ehrenbergiana</i> Hayne	-	Fabaceae	
<i>Acacia hockii</i> (ex: <i>flava</i>) De Wild.	-	Fabaceae	
<i>Acacia laeta</i> R. Br. ex Benth.	-	Fabaceae	
<i>Acacia macrostachya</i> Rchb. ex DC.	ACM	Fabaceae	Tchidi
<i>Acacia nilotica</i> (L.) Willd. ex Delile	ACN	Fabaceae	Gaoudi
<i>Acacia senegal</i> (L.) Willd.	ASN	Fabaceae	Patouki
<i>Acacia seyal</i> Delile	ASY	Fabaceae	Boulbi
<i>Acacia tortilis</i> subsp. <i>raddiana</i> (Savi) Brenan	ACT	Fabaceae	Tchili
<i>Adansonia digitata</i> L.	ADD	Malvaceae	Booki
<i>Adenium obesum</i> (Forssk.) Roem. et Schult	ADO	Apocynaceae	Darbouki
<i>Anogeissus leiocarpa</i> (DC.) Guill. et Perr.	ANL	Combretaceae	Kodioli
<i>Balanites aegyptiaca</i> (L.) Delile	BAA	Zygophyllaceae	Mourteki
<i>Bauhinia rufescens</i> Lam.	BAR	Fabaceae	Namaari
<i>Bombax costatum</i> Pellegr. & Vuillet	-	Malvaceae	
<i>Boscia senegalensis</i> (Pers.) Lam. ex Poir.	BOS	Capparaceae	Guidjili
<i>Bridelia ferruginea</i> Benth.	BRF	Phyllanthaceae	
<i>Calotropis procera</i> (Aiton) W.T. Aiton	CAP	Apocynaceae	Bawami
<i>Capparis decidua</i> (Forssk.) Edgew.	-	Capparaceae	
<i>Capparis tomentosa</i> Lam.	-	Capparaceae	
<i>Combretum aculeatum</i> Vent.	COA	Combretaceae	Laoniandi
<i>Combretum glutinosum</i> Perr. ex DC.	COG	Combretaceae	Dooki
<i>Commiphora africana</i> (A. Rich.) Engl.	COM	Burseraceae	Baddi
<i>Cordia sinensis</i> Lam.	COS	Boraginaceae	
<i>Dalbergia melanoxylon</i> Guill. et Perr.	DAM	Fabaceae	Dialambani
<i>Dichrostachys cinerea</i> (L.) Wight et Arn.	DIC	Fabaceae	
<i>Entada africana</i> Guill. et Perr.	ENA	Fabaceae	
<i>Euphorbia balsamifera</i> Aiton	EUB	Euphorbiaceae	

Table A1.1 – continued.

Species	Abbr.	Family	Fulani names
<i>Faidherbia albida</i> (Delile) A. Chev.	FAA	Fabaceae	Tiaski
<i>Feretia apodanthera</i> Delile	FEA	Rubiaceae	Tchiombi
<i>Grewia bicolor</i> Juss.	GRB	Malvaceae	Kelli
<i>Grewia flavescens</i> Juss.	GRF	Malvaceae	
<i>Guiera senegalensis</i> J. F. Gmel.	GUS	Combretaceae	Gueloki
<i>Lannea acida</i> A. Rich.	LAA	Anacardiaceae	Tchingoli
<i>Leptadenia hastata</i> (Pers.) Decne. ¹⁹	LEH	Apocynaceae	Tiapa toki
<i>Leptadenia pyrotechnica</i> (Forssk.) Decne.	LEP	Apocynaceae	Thim lodi
<i>Maerua angolensis</i> DC.	MAA	Capparaceae	Bagui
<i>Maerua crassifolia</i> Forssk.	-	Capparaceae	
<i>Maytenus senegalensis</i> (Lam.) Exell ²⁰	MAS	Celastraceae	Djialgotoi
<i>Mitragyna inermis</i> (Willd.) K. Schum.	MII	Rubiaceae	Koeli
<i>Piliostigma reticulatum</i> (DC.) Hochst.	PIR	Fabaceae	Barkedji
<i>Pterocarpus lucens</i> Lepr. ex Guill. et Perr.	-	Fabaceae	
<i>Salvadora persica</i> L.	-	Salvadoraceae	
<i>Sclerocarya birrea</i> (A. Rich.) Hochst.	SCB	Anacardiaceae	Heri
<i>Sterculia setigera</i> Delile	STS	Malvaceae	Bobori
<i>Stereospermum kunthianum</i> Cham.	STK	Bignoniaceae	Golombi
<i>Syzygium guineense</i> (Willd.) DC.	SYG	Myrtaceae	
<i>Terminalia avicennioides</i> Guill. et Perr.	TEA	Combretaceae	Poulemi
<i>Ziziphus mauritiana</i> Lam.	ZIM	Rhamnaceae	Diabi

¹⁹ Now *Leptadenia lanceolata* (Poir.) Goyder²⁰ Now *Gymnosporia senegalensis* (Lam.) Loes.

Appendix 2: Illustrations of the study area

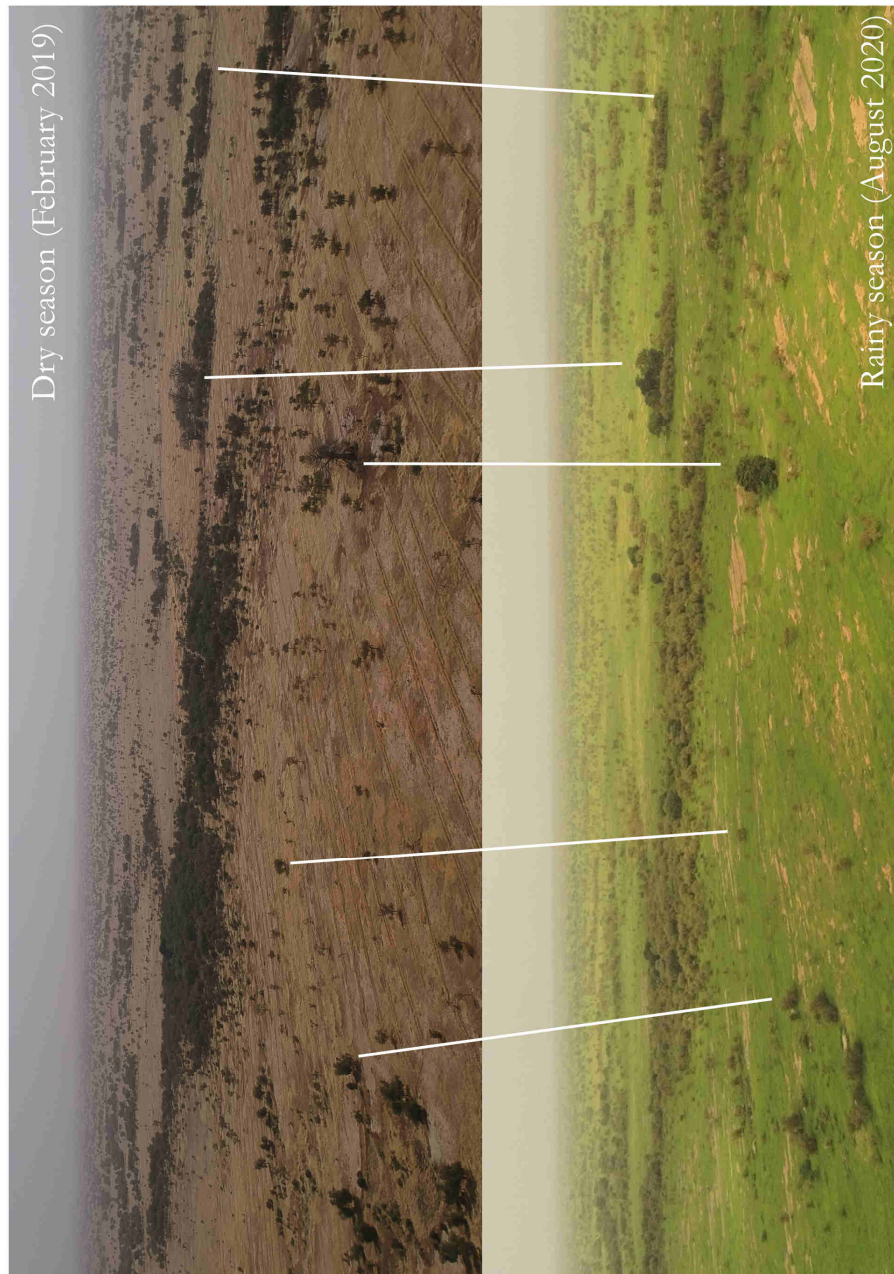


Figure A2.1 – Landscape near Widou Thiengoly (15.976562° N, 15.305688° W) during the dry and rainy seasons. Photos: S. Taugourdeau.



Figure A2.2 – Vegetation during the dry season. Photo: M. Dendoncker, April 2016.



Figure A2.3 – Vegetation at the end of the rainy season. Photo: M. Dendoncker, September 2015.



Figure A2.4 – Vegetation during the dry season near Widou Thiengoly. Photo: S. Taugourdeau, February 2019.



Figure A2.5 – Location of a depression in which a temporary pond is formed during the rainy season (where the soil is cracked), view from drone during the dry season. Photo: S. Taugourdeau, November 2018.



Figure A2.6 – Temporary pond near Tessékéré. Photo: M. Dendoncker, August 2015.



Figure A2.7 – Cattle drinking at a temporary pond. Photo: S. Taugourdeau, August 2019.



Figure A2.8 – Deep well of Widou Thiengoly. On the left, the hydraulic pump and the water tank. On the right, Widou village. Photo: M. Dendoncker, August 2015.



Figure A2.9 – Gathering of livestock at a water hole at the deep well of Widou Thiengoly at the beginning of the dry season. Photo: S. Taugourdeau, November 2018.

Appendix 3: Multivariate analyses used in this work

A3.1. Principal Components Analysis (PCA) and Principal Coordinates Analysis (PCoA)

Principal components analysis (PCA) and Principal Coordinates analysis (PCoA) are multivariate methods widely used in ecology to summarize and visualize large datasets of individuals described by several variables.

PCA performs a reduction in the number of explanatory quantitative variables by transforming the original variables with linear combinations. The principal components derived from the original variables are independent and retain the maximum information from the original dataset. The first principal components (the first two or three) can be graphically visualized and highlight the major differences between individuals. These components can subsequently be used in further analyses.

Principal Coordinates Analysis is a generalization of the PCA and, contrary to the PCA is based on a distance matrix. It allows to encompass all kind of descriptors, and not only quantitative one. In this work, it is used to represent botanical composition of a list of communities (using of Bray-Curtis distance, see below) and to represent species in traits space (using Gower distance, see below).

See Legendre and Legendre (2012) for further details.

A3.2. Distance and similarity measures in ecology

In ecology, it is frequent to want to assess the dissimilarity (or the resemblance) between objects (e.g. between inventory plots). A distance measure is the opposite of a similarity measure. According to the type of data (e.g. quantitative, like abundances or continuous traits value for a list of species; or ordinal, like categorical traits), we will use different measures.

In this work, we used two types of distance measures in order to assess the similarity between botanical records (e.g. an inventory plot) based on their species composition (which species is present in one plot, which are absent,

which are the common species) and the similarity between species based on their functional traits.

The data are organized in matrix. The objects between which we want to assess the similarity are in columns. The descriptors from which the similarity is assessed are in rows.

Example for the botanical composition of two inventory plots (A_{ij} represents the abundance or the presence of the species i in the plot j):

Inventory plot		Plot 1	Plot 2
<i>Species</i>	Sp_1	A_{11}	A_{12}
	Sp_2	A_{21}	A_{22}
	Sp_3	A_{31}	A_{32}

Example for traits values ($Trait_{ij}$ represents the value of trait i for the species j):

Species		Sp1	Sp2	Sp3
<i>Traits</i>	Tr_1	$Trait_{11}$	$Trait_{12}$	$Trait_{13}$
	Tr_2	$Trait_{21}$	$Trait_{22}$	$Trait_{23}$
	Tr_3	$Trait_{31}$	$Trait_{32}$	$Trait_{33}$

Euclidian distance: The Euclidian distance is equivalent to the Pythagoras' theorem for a space in multiple dimensions.

<i>Species</i>	Plot A	Plot B	$(A-B)^2$
$Sp1$	6	3	$(6-3)^2 = 9$
$Sp2$	5	1	$(5-1)^2 = 16$
$Sp3$	4	2	$(4-2)^2 = 4$

$$Euclidian\ distance = \sqrt{\sum (a - b)^2} = \sqrt{9 + 16 + 4} = \sqrt{29} = 5.4$$

Bray-Curtis distance: Bray-Curtis distance is the opposite of the Steinhaus similarity index (Bray-Curtis = 1 – Steinhaus).

<i>Species</i>	Plot A	Plot B	min(A,B)
$Sp1$	7	3	3
$Sp2$	8	2	2
$Sp3$	5	1	1
Sum	20 (a)	6 (b)	6 (w)

$$Bray - Curtis = 1 - Steinhaus_{A,B} = 1 - \left(\frac{2w}{(a + b)} \right) = 1 - \left(\frac{2 \times 6}{20 + 6} \right) \\ = 1 - 0.46$$

Gower distance: Useful for traits analysis because it allows different types of data (continuous, categorical, etc.).

<i>Species</i>	Plot A	Plot B	Plot C	A-B	Largest difference between any plot
<i>Sp1</i>	7	3	5	4	4
<i>Sp2</i>	8	2	0	6	8
<i>Sp3</i>	5	1	0	4	5

Example for the Gower distance between A and B:

For each species, we compute S_{pi} :

$$S_{pi} = 1 - \left(\frac{|A_i - B_i|}{\text{largest difference}} \right)$$

$$Gower_{A,B} = \text{moyenne}(S_{pi}) = \frac{\left(1 - \frac{4}{4}\right) + \left(1 - \frac{6}{8}\right) + \left(1 - \frac{4}{5}\right)}{3}$$

Appendix 4: Formulas of functional diversity indices

Table A4.1 – Description and formulas to compute FD indices used in this thesis (the lines for FRic, FEve, FDis and FDI are extracted from Legras *et al.*, 2019).

Index	Description	Formulas	Authors
FRic	Amount of functional space filled by the community	Quickhull algorithm (for the computation of convex hull)	Villéger <i>et al.</i> , 2008
FEve	Sum of MST (Minimum Spanning Tree) branch length (l) weighted by relative abundance	$\frac{\sum_{l=1}^{S-1} \min\left(PEW_l \frac{1}{S-1}\right) - \left(\frac{1}{S-1}\right)}{1 - \frac{1}{S-1}}$	Villéger <i>et al.</i> , 2008
FDiv	Species deviance from the mean distance to the center of gravity weighted by relative abundance	$\frac{\Delta d + \overline{dG}}{\Delta d + dG}$	Villéger <i>et al.</i> , 2008
FDis	Mean distance of individual species to the centroid of all species to the community	$\frac{\sum p_i z_i}{\sum p_i}$	Laliberté and Legendre, 2010
CWM	For one trait, mean of the trait values present in the community, weighted by the relative abundance of species presenting each value	$\sum_{i=1}^S p_i \times trait_i$	Lavorel <i>et al.</i> , 2008

With:

- S , total species richness (number of species);
- p_i , relative abundance of species i in the community;
- dG , mean distance of species to the center of gravity of the community;
- Δd , sum of abundance-weighted deviances;
- $\Delta|d|$, absolute abundance-weighted deviances from the center of gravity of the community;

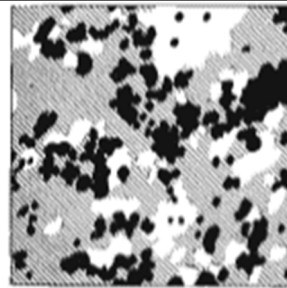
- PEW_i , partial weighted evenness; $PEW_l = \frac{\frac{dist(i,j)}{w_i+w_j}}{\sum_{l=1}^{S-1} \frac{dist(i,j)}{p_i+p_j}}$ for each branch l of the MST (Minimum Spanning Tree)
 - “MST is the tree that links all the points contained in a T-dimensional space with the minimum sum of branch lengths” (Villéger *et al.*, 2008);
 - With $dist(i,j)$: the Euclidian distance between species i and j .
- $\bar{x}_i$ distance of individual species to the centroid of the community;
- $trait_i$ trait value of species i .

Appendices to Chapter 3

Appendix 5: Landscape physiognomy

In an area of 250 km² around Fété-Olé, Bille *et al.* (1972) distinguish five landscape types according to different criteria: the presence of a sand layer; the shape, spacing and abundance of temporary ponds; the density and spatial distribution of trees; the aspect and extent of bare surfaces. It is a good illustration of the different types of landscape present inside the “sylvo-pastoral reserve of the six deep wells”. Landscapes within our study area mostly belong to the 3.1. and 3.2. categories. Blank area indicates patches of bare soil, dark area is the woody vegetation and grey hatched area is the herbaceous layer.

1. **Cuirass:** the surface layers are eroded, ferruginous concretions are found in surface, large surfaces with no vegetation, no particular arrangement of vegetation with the exception of temporary ponds.



0 100 500 m.
Echelle

2. Small dune systems

- 2.1. Non-oriented systems: small dunes without particular orientation, the relief is small. Temporary ponds are inside closed depressions with trees gathered around them. Vegetation is more homogeneous on the dunes.
- 2.2. Oriented systems: small parallel dunes, trees are gathered inside stretched depressions.

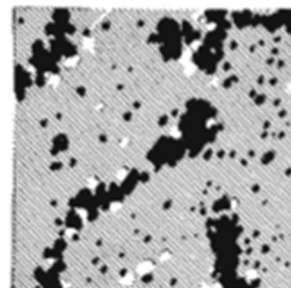
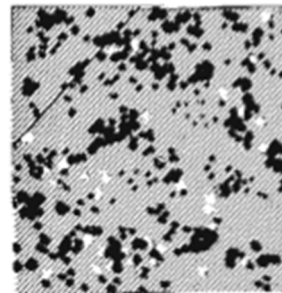
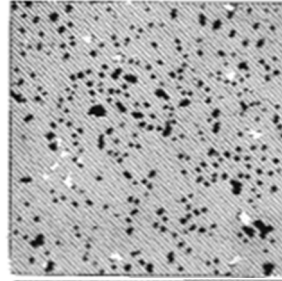


Figure A5.1 – Landscape physiognomy sketches from Bille *et al.* (1972).

3. Large dune systems

3.1. Dunes: length of several kilometers, width of 1-2 km, vegetation mostly spread regularly.



3.2. Interdunes: low, flat surfaces between dunes, trees gathered around temporary ponds.

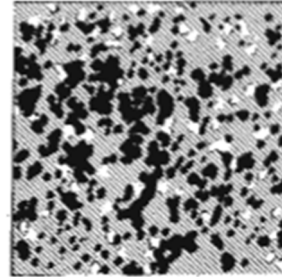


Figure A.5.1 – continued.

Appendix 6: Vegetation types inside the study area

A6.1. Description of the two vegetation units inside the study area, extract from Stancioff *et al.* (1986) – Chapter 5: Vegetation and land use

Description de l'unité Ac4 (pp. 535-537)

“Cette pseudo-steppe arbustive clairsemée couvre la majeure partie de l'erg précédent, qui, s'étant aplani au cours des siècles, s'est transformé en une pénéplaine avec des crêtes et des gouttières larges et allongées. L'unité Ac4 est généralement présente sur les sols sableux à argileux d'origine éolienne, et ouvre les pentes et les hauteurs du sud du Ferlo sableux.

La majorité de la végétation est protégée des pratiques culturales puisqu'une grande partie de ce type de couverture est située à l'intérieur de la Réserve sylvopastorale des six forages. Cette réserve de même que d'autres, réduit l'agriculture à une activité de subsistance pour les bergers qui cultivent quelques cultures alimentées par les eaux des pluies et l'a limitée à une exploitation des herbages. Une série de pare-feux traversent cette zone. Ils ont été introduits afin de protéger les pâturages contre les feux de brousse, qui sont souvent le fait de la main humaine. Au cours des trente dernières années, l'environnement s'est considérablement transformé du fait de la présence des troupeaux toute l'année. Ce changement est particulièrement perceptible autour des points d'eau, le piétinement constant, le surpâturage et le prélèvement des branches des arbres ont causé une dégradation qualitative et quantitative de la couverture végétale.

De rares arbres épars sont de règle. Ils sont dominés par des *Sclerocarya birrea*, *Balanites aegyptiaca* et *Combretum glutinosum*. Les arbustes et arbres de petite taille appartiennent aux espèces précédentes en plus de *Guiera senegalensis*, un intrus commun à toutes les zones perturbées. Leur sont associés *Boscia senegalensis*, *Acacia senegal*, *Calotropis procera* et *Terminalia avicennioides*. La végétation herbacée est composée des graminées *Eragrostis tremula*, *Cenchrus biflorus* et *Dactyloctenium aegyptium* et des espèces non graminéennes, *Alysicarpus ovalifolius*, *Zornia glochidiata* et *Borreria radiata*. Les espèces ligneuses couvrent 2 à 3% du sol, les arbres atteignant 5 à 7 m et les arbustes 1 à 3 m.

Beaucoup des espèces citées ci-dessus ont disparu des régions dégradées autour des points d'eau. Les espèces plus résistantes et celles qui sont moins appétissantes, comme *Boscia senegalensis*, *Ziziphus mauritiana*, *Guiera senegalensis* (un intrus), *Balanites aegyptiaca* (résistant au feu) et *Combretum glutinosum* (très rarement recherché par les animaux) quant à elles subsistent. ”

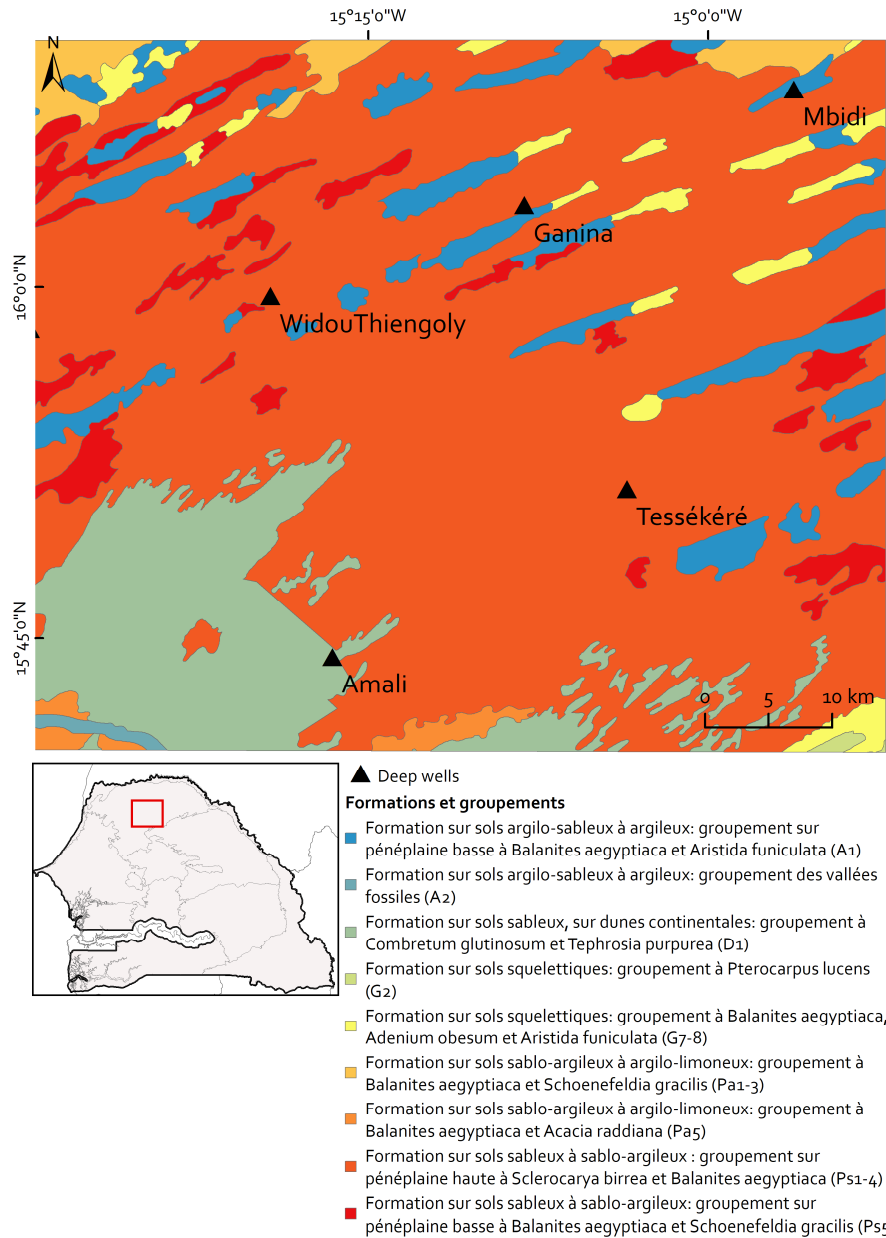
Description de l'unité Acm5 (p. 537)

“Cette unité est présente en association avec la précédente (Ac4) dans les vastes dépressions inter dunaires allongées de la pénéplaine du Ferlo sableux. Les sols sont des limons compacts et sableux. Entre les dépressions interdunaires on rencontre une multitude de petites dépressions, dont certaines sont inondées pendant la saison des pluies. Les communautés végétales sont formées d'espèces complètement différentes de celles poussant sur les hauteurs. Dans les dépressions s'est développée une couverture boisée dense, semblable à une savane boisée, tandis que les sols compacts entre ces dépressions (mais toujours dans les interdunes) sont couverts par une steppe arbustive clairsemée (...). Les arbres dans ces mares temporaires sont essentiellement des *Balanites aegyptiaca* (une espèce présente dans tout le nord du Ferlo), des *Acacia seyal*, des *Adansonia digitata* (qui apparaissent relativement géants dans ce groupement), des *Acacia adansonii*²¹ et *Sclerocarya birrea*. Les arbustes et les arbres de moindre taille dominent la strate ligneuse et sont des *Boscia senegalensis*, *Balanites aegyptiaca*, *Guiera senegalensis*, et *Calotropis procera* (tous communs), ou des *Ziziphus mauritiana*, *Commiphora* et *Grewia bicolor* (associés). La strate herbacée est communément composée de *Schoenefeldia gracilis*, *Eragrostis tremula*, *Alysicarpus ovalifolius* et *Zornia glochidiata*.

Les dépressions boisées sont généralement moins dégradées par les animaux et l'homme que les zones plus élevées. Les pâturages sont de bonne qualité sur les bords des dépressions et de mauvaise qualité sur les limons compacts entre les dépressions.”

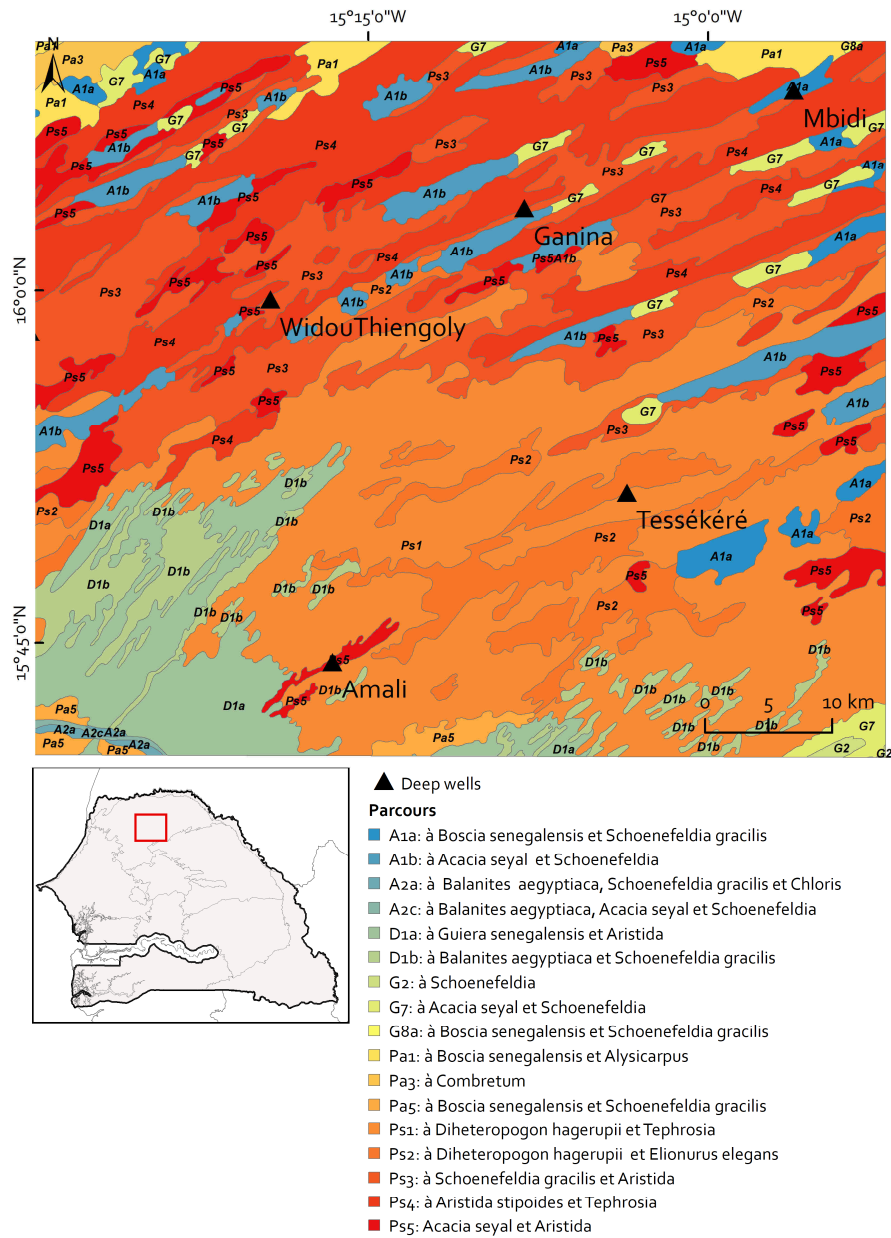
²¹ *Acacia nilotica*

A6.2. Classification of Valenza and Diallo (1972b)



UTM Zone 28N - Author: M. Dendoncker

Figure A6.1 – Vegetation classification (“formations” and “groupements”) according to Valenza and Diallo (1972b) inside the study area. The shapefile has been created based on a map that was georeferenced and digitalized.



UTM Zone 28N - Author: M. Dendoncker

Figure A6.2 – Vegetation classification (“parcours”) according to Valenza and Diallo (1972b) inside the study area. The shapefile has been created based on a map that was georeferenced and digitalized.

Appendix 7: Soils, topography and water content

The retention capacity (the maximum water content that the soil can retain) was estimated by Cornet from soil grain size and organic matter content. The difference between the humidity at the wilting point (pF 4.2, red curve) and the field capacity (pF 2.5, orange curve) represents the available water.

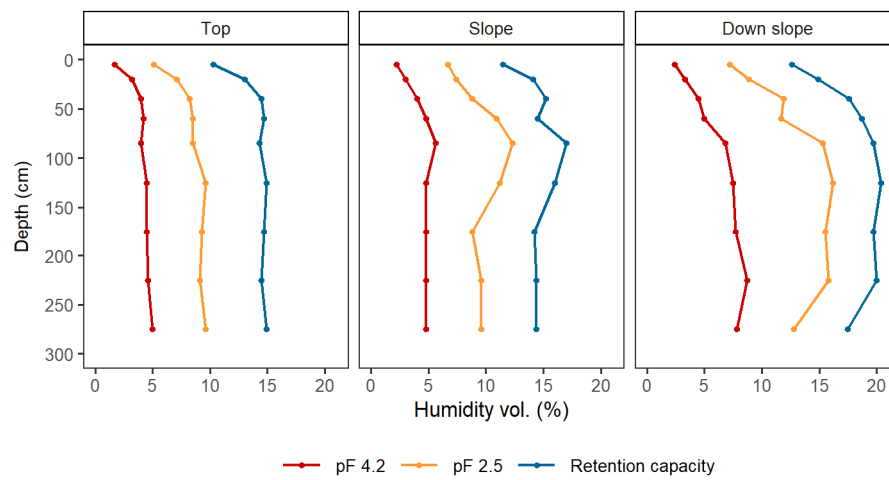


Figure A7.1 – Humidity profiles at pF 2.5 (field capacity), 4.2 (wilting point) and at retention capacity for three topographic elements. Created with data from Cornet (1981).

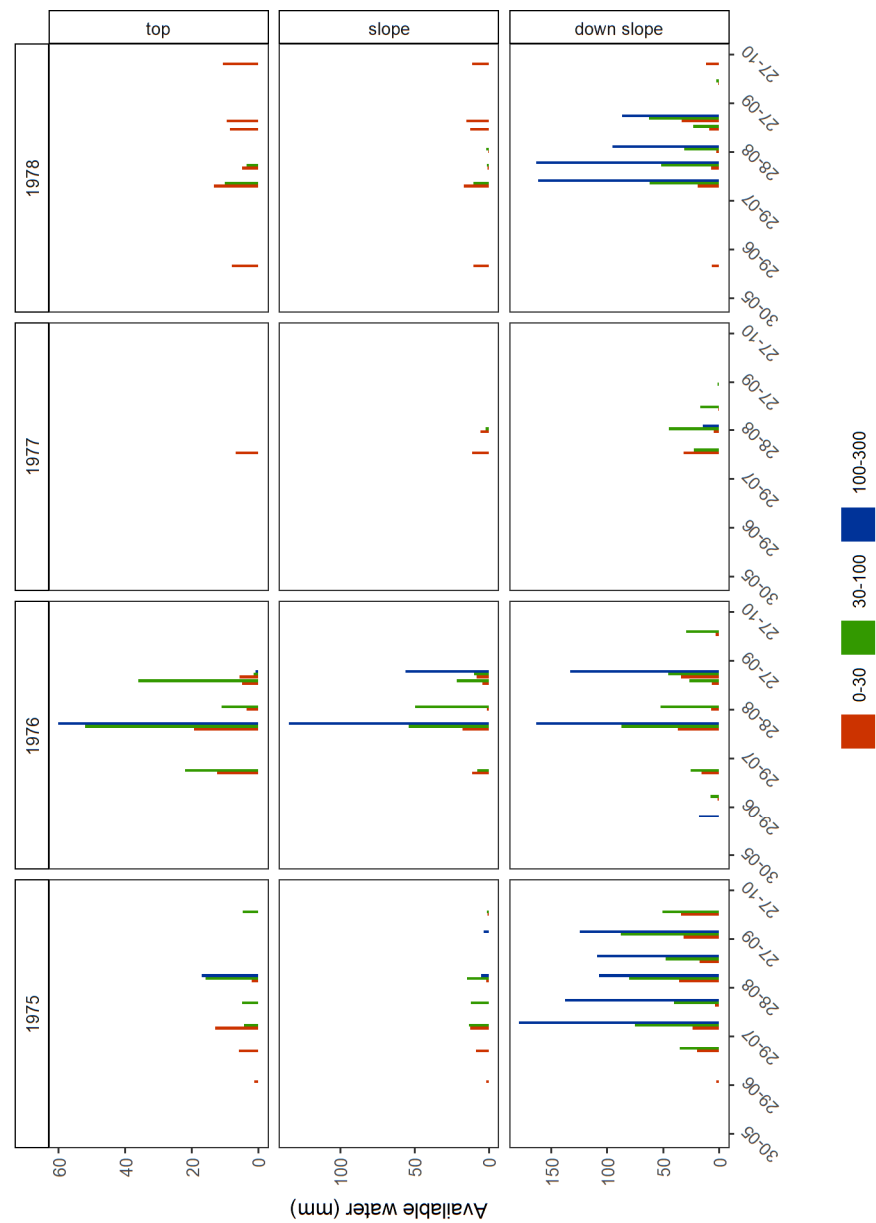


Figure A7.2 – Evolution of the available water content (mm) in three soil horizons (0-30 cm, 30-100 cm, 100-300 cm) on top, slope and down slope from 1975 to 1978.

Created with data from Cornet (1981).

Appendix 8: Climatic indicators

Three supplementary rainfall indicators are presented in Figure A8.1 and Figure A8.2. The mean gap between two rainy episodes is the duration in days between two rainy days. The simple daily intensity index (SDII; Frich *et al.*, 2002) represents the amount of water falling per rainy day. The Sahelian rainfall index corresponds, for each year, to the rainfall minus the average divided by standard deviation (L'Hote *et al.*, 2002).

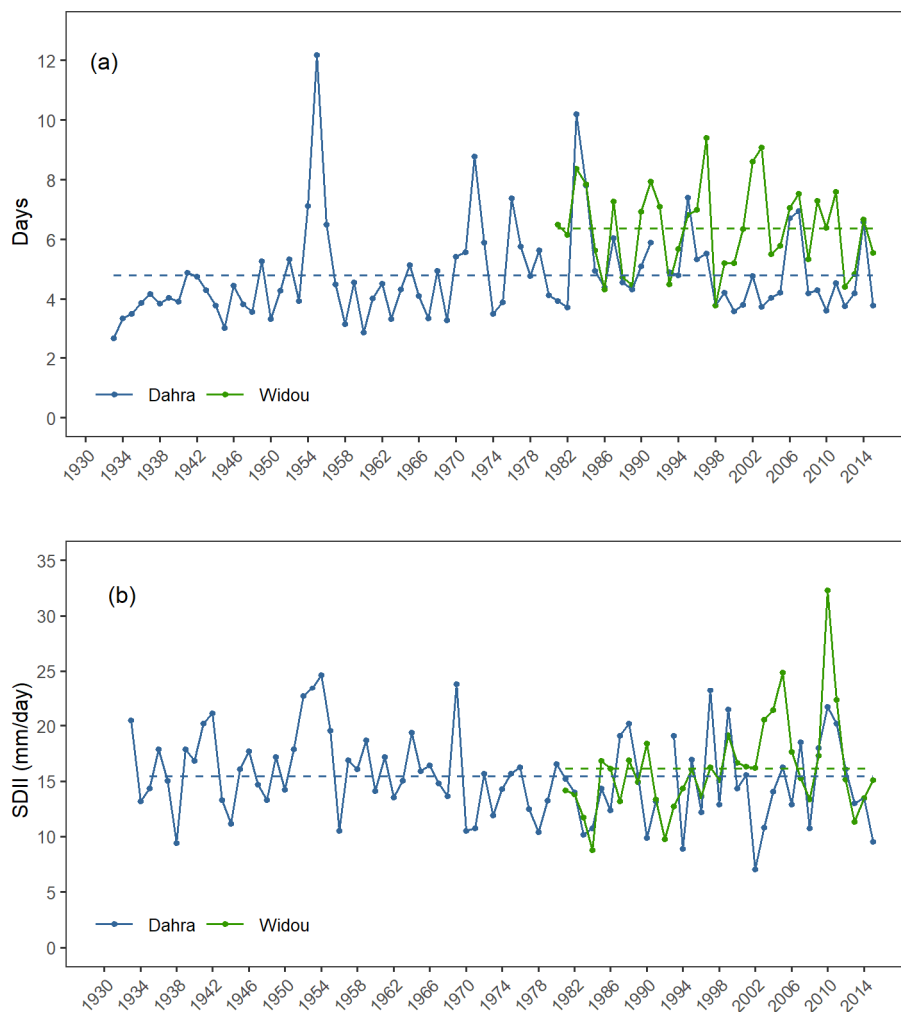


Figure A8.1 – (a) Mean gap between two rainy days (> 1 mm) and (b) simple daily intensity index (SDII) in Dahra and Widou. Dashed lines represent the means of the series.

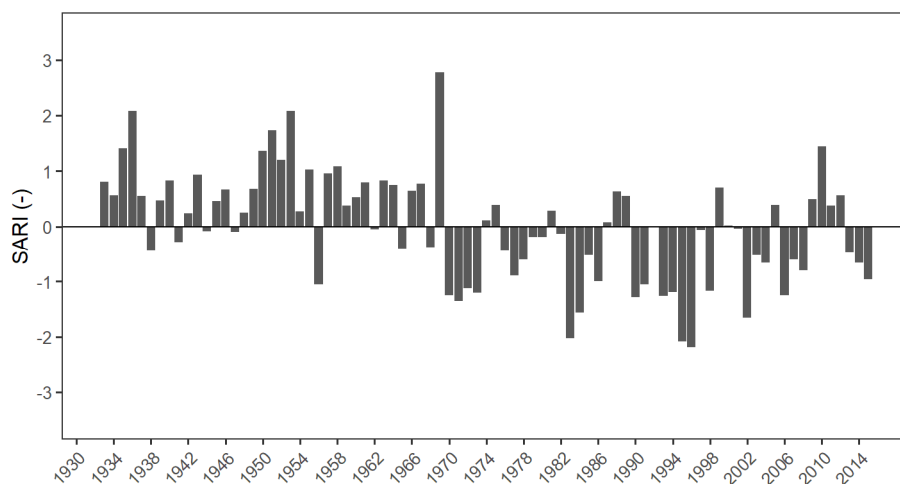


Figure A8.2 – Sahelian annual rainfall index (SARI) in Dahra.

Table A8.1 – Indicators based on rainfall data (number of rainy days, simple daily intensity index and mean gap between two rainy days) for the stations of Dagana, Dahra, Linguère (1933-2002) and Widou (1981-2015). Between brackets, years during which the extremes (max-min) were recorded.

Station	Mean ($\pm$ sd)	Maximum	Minimum
Number of rainy days			
Dagana	19.8 ($\pm$ 6.0)	37 (1955)	9 (1984)
Dahra	27.6 ($\pm$ 8.4)	45 (1935)	6 (1995)
Linguère	31.6 ($\pm$ 7.9)	55 (1951)	17 (1972)
Widou	18.1 ($\pm$ 3.9)	30 (1989)	9 (1983)
Simple daily intensity index (mm.day⁻¹)			
Dagana	13.5 ($\pm$ 3.8)	26.7 (1993)	3.6 (1983)
Dahra	15.6 ($\pm$ 3.7)	24.7 (1954)	8.9 (1994)
Linguère	14.2 ($\pm$ 3.2)	23.0 (1947)	9.0 (1983)
Widou	16.2 ($\pm$ 4.5)	32.3 (2010)	8.8 (1984)
Mean gap between two rainy days (days)			
Dagana	6.8 ($\pm$ 3.2)	18.8 (1991)	3 (1947)
Dahra	5.0 ($\pm$ 1.6)	12.2 (1955)	2.9 (1960)
Linguère	4.7 ($\pm$ 1.5)	10.6 (1972)	2.9 (1961)
Widou	6.3 ($\pm$ 1.4)	9.4 (1997)	3.8 (1998)
Length of the rainy season (days)			
Dagana	72.7 ($\pm$ 30.1)	124 (1955)	0 (1972)
Linguère	104.8 ($\pm$ 23.0)	160 (1943)	29 (1983)
Widou	79.1 ($\pm$ 25.3)	117 (2011)	0 (1984)

Appendix 9: Fulani camps recording

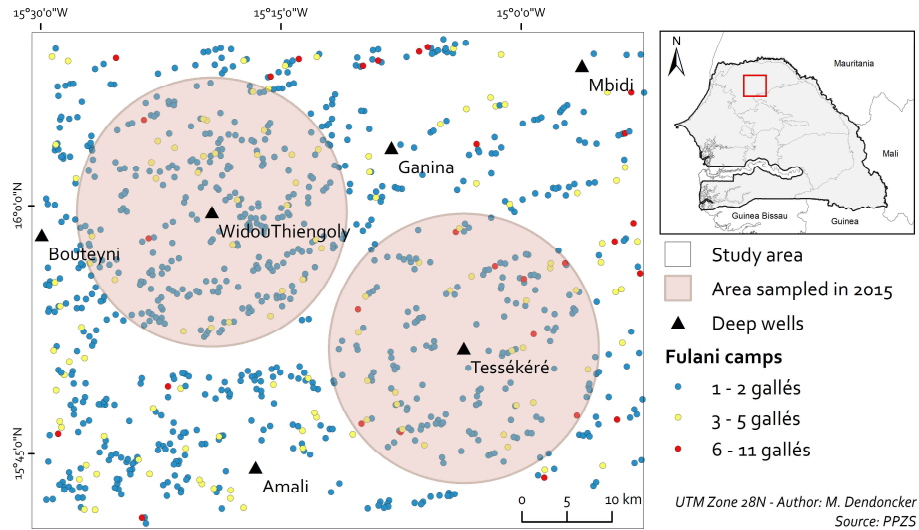


Figure A9.1 – Fulani camps recorded on Bing images of 2013, classified according to the number of galls.

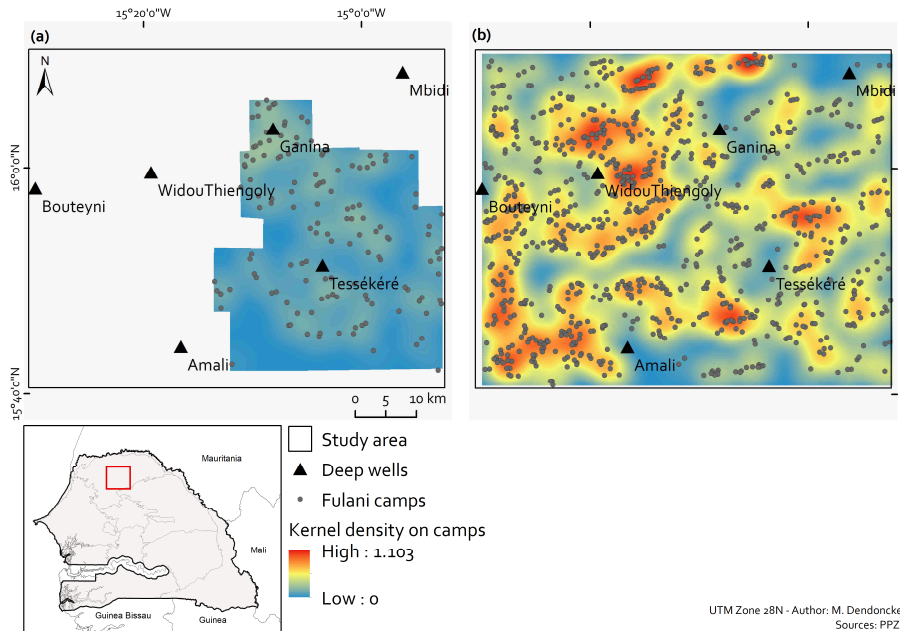


Figure A9.2 – Kernel density on the Fulani camps (a) in 1980 and (b) in 2013.

Table A9.1 – Estimation of the human population in 2013 within the service areas (15 km radius) of Widou Thiengoly and Tessékéré deep wells.

	Widou	Tessékéré	Total
Number of camps	279	177	456
Number of gallés	321	404	725
Mean number of gallés per camp	1.2	2.3	1.6
Estimation of the number of persons	4000	3178	7178
Density of the camps (camps.km ⁻²)	0.39	0.25	0.32

Appendix 10: Metadata on the inventoried plots in 2015-2017

The two following tables present the coordinates of the plots inventoried in 2015 and in 2017 along with some environmental characteristics such as soil or topography. Four plots located at 1 km were inventoried in 2015 but were not integrated to our analyses.

Table A10.1 – Plots inventoried in 2015. The plot id comprises three parts: the first letter indicates if the plot is near Tessékéré (T) or Widou (W); the first number indicates the distance from the deep well in km (3, 5 and 12 corresponding to 3.5, 5.5 and 12.5 km); the second number indicates the plots number inside its category of distance. Coordinates are in decimal degrees. “Topo” indicates if the plot is on a hilltop (T) or in a depression (D). The “Soil” column refers to the classification of the World Reference Base for Soil Resources (Jones *et al.*, 2013): “brunic” stands for brunic arenosols (subarid brown soil) and “ferralic” stands for ferralic arenosols (ferruginous tropical soils). The column “distance” explicitly gives the distance to the nearest deep wells (between Widou and Tessékéré). The “Rg” column indicates if the regeneration analysis has been carried out on the plot.

Plot id	Coordinates		Topo	Soil	Distance (km)	Rg
	Latitude	Longitude				
T.01.01	15.86209	-15.06746	T	brunic	1	no
T.01.02	15.86018	-15.070528	D	brunic	1	no
T.02.01	15.86475	-15.0769	D	brunic	2	no
T.02.02	15.86545	-15.075215	T	brunic	2	no
T.02.03	15.86893	-15.044497	T	brunic	2	yes
T.02.04	15.86739	-15.04428	T	brunic	2	yes
T.02.05	15.84386	-15.04365	D	ferralic	2	yes
T.02.06	15.84789	-15.042942	T	ferralic	2	yes
T.02.07	15.84045	-15.06382	T	ferralic	2	yes
T.02.08	15.83743	-15.0634	D	ferralic	2	yes
T.02.09	15.85003	-15.078207	T	ferralic	2	yes
T.02.10	15.84598	-15.07462	T	ferralic	2	yes
T.03.01	15.86973	-15.08586	D	ferralic	3.5	no
T.03.02	15.87204	-15.088341	T	ferralic	3.5	no
T.03.03	15.87780	-15.035177	T	brunic	3.5	yes
T.03.04	15.87434	-15.03285	T	brunic	3.5	yes
T.03.05	15.84133	-15.032967	D	ferralic	3.5	yes
T.03.06	15.83840	-15.032966	T	ferralic	3.5	yes
T.03.07	15.82553	-15.059982	T	ferralic	3.5	yes
T.03.08	15.82502	-15.05836	D	ferralic	3.5	yes
T.03.09	15.83941	-15.086318	T	ferralic	3.5	yes

Table A10.1 – continued.

Plot id	Coordinates		Topo	Soil	Distance (km)	Rg
	Latitude	Longitude				
T.03.10	15.84053	-15.08799	T	ferralic	3.5	yes
T.05.01	15.87744	-15.099315	D	ferralic	5	no
T.05.02	15.87773	-15.100776	T	ferralic	5	no
T.05.03	15.88338	-15.02385	D	brunic	5	yes
T.05.04	15.88541	-15.02322	D	brunic	5	yes
T.05.05	15.83782	-15.01761	T	ferralic	5	yes
T.05.06	15.83147	-15.02101	T	ferralic	5	yes
T.05.07	15.81201	-15.067888	T	brunic	5	yes
T.05.08	15.81208	-15.067229	T	brunic	5	yes
T.05.09	15.83356	-15.10113	D	ferralic	5	yes
T.05.10	15.83391	-15.100186	T	ferralic	5	yes
T.07.01	15.88913	-15.122522	D	ferralic	7.5	no
T.07.02	15.88811	-15.124037	T	ferralic	7.5	no
T.07.03	15.89588	-15.00212	D	brunic	7.5	yes
T.07.04	15.89471	-15.00137	T	brunic	7.5	yes
T.07.05	15.84073	-14.99268	D	ferralic	7.5	yes
T.07.06	15.83719	-14.991896	T	ferralic	7.5	yes
T.07.07	15.78936	-15.065	T	brunic	7.5	yes
T.07.08	15.78937	-15.067607	T	brunic	7.5	yes
T.07.09	15.82007	-15.11879	T	ferralic	7.5	yes
T.07.10	15.82171	-15.119898	T	ferralic	7.5	yes
T.10.01	15.89985	-15.141524	T	ferralic	10	no
T.10.02	15.89773	-15.14322	T	ferralic	10	no
T.10.03	15.90947	-14.98338	D	brunic	10	yes
T.10.04	15.90903	-14.98211	T	brunic	10	yes
T.10.05	15.80915	-14.97941	T	brunic	10	yes
T.10.06	15.81221	-14.98039	D	brunic	10	yes
T.10.07	15.76755	-15.070817	T	ferralic	10	yes
T.10.08	15.76740	-15.06807	T	ferralic	10	yes
T.10.09	15.80807	-15.137845	D	ferralic	10	yes
T.10.10	15.80828	-15.138518	T	ferralic	10	yes
T.12.01	15.90459	-15.166484	D	ferralic	12	no
T.12.02	15.90315	-15.166001	T	ferralic	12	no
T.12.03	15.92781	-14.96881	T	ferralic	12.5	yes
T.12.04	15.92860	-14.96868	D	ferralic	12.5	yes
T.12.05	15.79394	-14.96227	T	ferralic	12.5	yes
T.12.06	15.79587	-14.96108	T	ferralic	12.5	yes
T.12.07	15.74346	-15.067233	T	ferralic	12.5	yes
T.12.08	15.74382	-15.068547	T	ferralic	12.5	yes
T.12.09	15.79955	-15.16087	D	ferralic	12.5	yes
T.12.10	15.79879	-15.160084	T	ferralic	12.5	yes
T.15.01	15.91992	-15.182991	T	ferralic	15	no
T.15.02	15.93399	-15.17501	T	ferralic	15	no

Table A10.1 – continued.

Plot id	Coordinates		Topo	Soil	Distance (km)	Rg
	Latitude	Longitude				
T.15.03	15.93838	-14.94822	T	ferralic	15	yes
T.15.04	15.93746	-14.94762	D	ferralic	15	yes
T.15.05	15.78109	-14.94407	D	brunic	15	yes
T.15.06	15.78195	-14.94332	T	brunic	15	yes
T.15.07	15.72260	-15.07477	T	brunic	15	yes
T.15.08	15.72168	-15.072552	T	brunic	15	yes
T.15.09	15.78488	-15.179488	D	ferralic	15	yes
T.15.10	15.78822	-15.179605	T	ferralic	15	yes
W.01.03	15.98900	-15.313647	D	ferralic	1	no
W.01.04	15.98959	-15.31341	T	ferralic	1	no
W.02.01	15.99930	-15.304054	T	ferralic	2	no
W.02.02	16.00114	-15.30465	D	ferralic	2	no
W.02.03	15.98507	-15.3060	T	ferralic	2	no
W.02.04	15.98618	-15.305137	T	ferralic	2	no
W.02.05	15.97629	-15.32504	T	brunic	2	no
W.02.06	15.97668	-15.327008	T	brunic	2	no
W.02.07	15.99538	-15.340035	T	ferralic	2	yes
W.02.08	15.98213	-15.33504	D	brunic	2	yes
W.02.09	16.01214	-15.321055	T	ferralic	2	no
W.02.10	16.01137	-15.32655	D	ferralic	2	no
W.03.01	15.99789	-15.288769	T	ferralic	3.5	no
W.03.02	16.01736	-15.300156	T	brunic	3.5	no
W.03.03	15.98060	-15.291961	D	brunic	3.5	no
W.03.04	15.98038	-15.294073	T	brunic	3.5	no
W.03.05	15.96391	-15.331757	T	ferralic	3.5	no
W.03.06	15.96634	-15.33318	D	ferralic	3.5	no
W.03.07	15.98668	-15.354057	T	ferralic	3.5	yes
W.03.08	15.97711	-15.34954	T	brunic	3.5	yes
W.03.09	16.02551	-15.32301	D	brunic	3.5	no
W.03.10	16.02660	-15.324261	T	brunic	3.5	no
W.05.01	16.00764	-15.27621	D	ferralic	5	no
W.05.02	16.01146	-15.278291	T	brunic	5	no
W.05.03	15.96970	-15.276247	D	brunic	5	no
W.05.05	15.94888	-15.328299	T	ferralic	5	no
W.05.06	15.94898	-15.325829	T	ferralic	5	no
W.05.07	15.97204	-15.361832	T	brunic	5	yes
W.05.08	15.97062	-15.36164	D	brunic	5	yes
W.05.09	16.03923	-15.324906	T	brunic	5	no
W.05.10	16.03842	-15.32864	T	brunic	5	no
W.07.01	16.02094	-15.2563	D	ferralic	7.5	no
W.07.02	16.02385	-15.25932	T	brunic	7.5	no
W.07.03	15.95641	-15.257883	T	ferralic	7.5	no
W.07.04	15.95428	-15.264806	T	ferralic	7.5	no

Table A10.1 – continued.

Plot id	Coordinates		Topo	Soil	Distance (km)	Rg
	Latitude	Longitude				
W.07.05	15.92787	-15.33336	T	ferralic	7.5	no
W.07.06	15.92750	-15.33395	T	ferralic	7.5	no
W.07.07	15.96069	-15.383059	T	brunic	7.5	yes
W.07.08	15.95630	-15.38253	D	brunic	7.5	yes
W.07.09	16.06058	-15.33309	D	ferralic	7.5	no
W.07.10	16.06127	-15.32942	T	ferralic	7.5	no
W.10.01	16.03050	-15.234454	T	ferralic	10	no
W.10.02	16.03059	-15.235888	T	ferralic	10	no
W.10.03	15.94687	-15.239625	T	brunic	10	no
W.10.04	15.94806	-15.24006	D	brunic	10	no
W.10.05	15.90269	-15.326537	T	brunic	10	no
W.10.06	15.90405	-15.333301	T	brunic	10	no
W.10.07	15.95205	-15.40492	D	ferralic	10	yes
W.10.08	15.95619	-15.40627	T	ferralic	10	yes
W.10.09	16.08217	-15.3371	D	brunic	10	no
W.10.10	16.08299	-15.33771	T	brunic	10	no
W.12.01	16.04566	-15.21756	T	ferralic	12.5	no
W.12.02	16.04244	-15.21585	T	ferralic	12.5	no
W.12.03	15.94301	-15.216841	T	ferralic	12.5	no
W.12.04	15.93589	-15.22183	T	ferralic	12.5	no
W.12.05	15.88182	-15.336397	D	brunic	12.5	no
W.12.06	15.88133	-15.331199	T	brunic	12.5	no
W.12.07	15.95162	-15.430316	T	ferralic	12.5	yes
W.12.08	15.95245	-15.42853	D	ferralic	12.5	yes
W.12.09	16.10453	-15.34364	D	ferralic	12.5	no
W.12.10	16.10633	-15.33382	T	ferralic	12.5	no
W.15.01	16.05516	-15.196433	T	ferralic	15	no
W.15.02	16.05087	-15.194225	T	ferralic	15	no
W.15.03	15.89295	-15.23178	D	ferralic	15	no
W.15.04	15.94359	-15.191372	T	ferralic	15	no
W.15.05	15.85863	-15.33591	T	brunic	15	no
W.15.06	15.85982	-15.33499	D	brunic	15	no
W.15.07	15.93491	-15.44804	T	ferralic	15	yes
W.15.08	15.92657	-15.44122	D	brunic	15	yes
W.15.09	16.12919	-15.32436	T	brunic	15	no
W.15.10	16.12952	-15.32216	T	brunic	15	no

Table A10.2 – Plots inventoried in December 2017. The column “Site id” corresponds to the study sites of 1 km² considered in Chapter 5. “Topo” indicates the local topography.

Plot	Plot id	Coordinates		Site id	Relief	Topo
		Latitude	Longitude			
1	p2017.01	15.862678	-14.953070	HC_d_03	dune	top
2	p2017.02	15.869019	-14.947524	HC_d_03	dune	slope
3	p2017.03	15.869856	-14.951677	HC_d_03	dune	slope
4	p2017.04	15.863568	-14.946529	HC_d_03	dune	slope
5	p2017.05	15.862717	-14.949332	HC_d_03	dune	slope
6	p2017.06	15.880271	-15.083210	HC_d_01	dune	top
7	p2017.07	15.878489	-15.088843	HC_d_01	dune	top
8	p2017.08	15.875304	-15.089214	HC_d_01	dune	top
9	p2017.09	15.882543	-15.090221	HC_d_01	dune	top
10	p2017.10	15.847187	-14.994353	HC_d_04	dune	slope
11	p2017.11	15.880740	-15.090687	HC_d_01	dune	slope
12	p2017.12	15.924445	-15.101076	HC_d_02	dune	slope
13	p2017.13	15.919463	-15.100125	HC_d_02	dune	slope
14	p2017.14	15.880750	-15.086940	HC_d_01	dune	top
15	p2017.15	15.881660	-15.089283	HC_d_01	dune	slope
16	p2017.16	15.802401	-15.174922	HC_p_03	plain	depression
17	p2017.17	15.919779	-15.044779	HC_p_02	plain	top
18	p2017.18	15.803354	-15.178258	HC_p_03	plain	top
19	p2017.19	15.917047	-15.039630	HC_p_02	plain	depression
20	p2017.20	15.912084	-15.046175	HC_p_02	plain	depression
21	p2017.21	15.958747	-15.085668	HC_p_04	plain	depression
22	p2017.22	15.956533	-15.083325	HC_p_04	plain	depression
23	p2017.23	15.816894	-15.078006	HC_p_01	plain	slope
24	p2017.24	15.954262	-15.079156	HC_p_04	plain	slope
25	p2017.25	15.814541	-15.081602	HC_p_01	plain	top
26	p2017.26	15.959207	-15.084279	HC_p_04	plain	depression
27	p2017.27	15.957487	-15.080120	HC_p_04	plain	depression
28	p2017.28	15.956049	-15.083821	HC_p_04	plain	top
29	p2017.29	15.811595	-15.078171	HC_p_01	plain	depression
30	p2017.30	15.959167	-15.081048	HC_p_04	plain	top

Appendix 11: List of some GIS data collected

Table A11.1 – List of the GIS data (non-exhaustive) collected classified according to their spatial coverage (Senegal, Ferlo, study area).

Name	Description and source	Treatment
Senegal		
Ecoregions	Boundaries of the ecological regions as defined by Tappan <i>et al.</i> , 2004. Provided by the University of Copenhagen.	
Ferlo		
Vegetation types Valenza	Vegetation types according to Valenza and Diallo (1972a).	Georeferencing of the map and digitalization in polygons.
Vegetation types Tappan	Vegetation types according to Tappan (1986).	Georeferencing of the map and digitalization in polygons.
Morphopedology	Morphopedology according to Stancioff <i>et al.</i> (1986).	Georeferencing of the map and digitalization in polygons.
Deep wells	Location of deep wells in the Ferlo; mixed sources.	Several shapefiles have been aggregated and each point was visually check and compare with Bing map.
Corona images	Images were taken the 26 th of December 1965 Scenes IDs: DS1028-1027DA016_b DS1028-1027DA017_b DS1028-1027DA018_b DS1028-1027DA019_b DS1028-1027DA016_c	Georeferencing

Table A11.1 – continued.

Name	Description and source	Treatment
<i>Ferlo</i>		
Aerial photos (<i>n</i> = 31)	Scenes IDs: 511_29_502045; 511_30_502179; 511_30_502181; 511_30_502183 513_31_502383; 513_31_502385 513_31_502387; 513_32_502449 513_32_502449; 513_32_502453 513_32_502455; 513_33_502613 513_33_502615; 513_33_502617 513_33_502619 Lower quality : 511_29_502038; 511_29_502039 511_29_502040; 511_29_502041 511_29_502042; 511_29_502043 511_29_502044; 511_30_502171 511_30_502172; 511_30_502173 511_30_502174; 511_30_502177 511_32_502445; 513_32_502446 513_32_502447; 513_32_502448	Georeferencing
<i>Study area</i>		
Fulani camps	Recorded in the frame of this work, available for 1980 (Tessékéré area), 2008, 2013 (all study area).	

Appendix 12: Species list researched for traits values

Table A12.1– Species for which traits values were collected.

Species	Abbreviation	Reason for which the species is investigated
<i>Acacia ataxacantha</i>	ACA	Recorded in 2015
<i>Acacia erythrocalyx</i>	ACE	Recorded in Flotrop
<i>Acacia macrostachya</i>	ACM	Recorded in Flotrop
<i>Acacia nilotica</i>	ACN	Recorded in 2015
<i>Acacia senegal</i>	ASN	Recorded in 2015
<i>Acacia seyal</i>	ASY	Recorded in 2015
<i>Acacia tortilis</i>	ACT	Recorded in 2015
<i>Adansonia digitata</i>	ADD	Recorded in 2015
<i>Adenium obesum</i>	ADO	Recorded in 2015
<i>Anogeissus leiocarpa</i>	ANL	Recorded in 2015
<i>Balanites aegyptiaca</i>	BAA	Recorded in 2015
<i>Bauhinia rufescens</i>	BAH	Recorded in 2015
<i>Boscia senegalensis</i>	BOS	Recorded in 2015
<i>Bridelia ferruginea</i>	BRF	Recorded in Flotrop
<i>Calotropis procera</i>	CAP	Recorded in 2015
<i>Combretum aculeatum</i>	COA	Recorded in 2015
<i>Combretum glutinosum</i>	COG	Recorded in 2015
<i>Commiphora africana</i>	COM	Recorded in 2015
<i>Cordia sinensis</i>	COS	Recorded in Flotrop
<i>Dalbergia melanoxylon</i>	DAM	Recorded in 2015
<i>Dichrostachys cinerea</i>	DIC	Recorded in Flotrop
<i>Entada africana</i>	ENA	Recorded in Flotrop
<i>Faidherbia albida</i>	FAA	Recorded in 2015
<i>Feretia apodanthera</i>	FEA	Recorded in 2015
<i>Grewia bicolor</i>	GRB	Recorded in 2015
<i>Grewia flavescens</i>	BRF	Recorded in Flotrop
<i>Guiera senegalensis</i>	GUS	Recorded in 2015
<i>Lannea acida</i>	LAA	Recorded in Flotrop
<i>Leptadenia pyrotechnica</i>	LEP	Recorded in 2015
<i>Maerua angolensis</i>	MAA	Recorded in Flotrop
<i>Maytenus senegalensis</i>	MAS	Recorded in Flotrop
<i>Mitragyna inermis</i>	MII	Recorded in Flotrop
<i>Piliostigma reticulatum</i>	PIR	Recorded in Flotrop
<i>Sclerocarya birrea</i>	SCB	Recorded in 2015
<i>Sterculia setigera</i>	STS	Recorded in Flotrop
<i>Stereospermum kunthianum</i>	STK	Recorded in 2015
<i>Syzygium guineense</i>	SYG	Recorded in Flotrop
<i>Terminalia avicennioides</i>	TEA	Recorded in Flotrop
<i>Ziziphus mauritiana</i>	ZIM	Recorded in 2015

Note: the species *Euphorbia balsamifera* recorded in Flotrop was not taken into account, as it does not belong to spontaneous vegetation. It is the same for *Leptadenia hastata*, as it was excluded in our analyses in Chapter 4, it was not included in the trait-based approach.

Appendix 13: Sources for response and effect traits

Table A13.1 – Traits linked to the three studied pressures according to the literature, mechanisms (only if they were clearly enounced in literature) and sources. The stars indicate the traits that were used in this study. The other traits were not used because of a lack of data.

Response traits	Mechanisms	Sources
Grazing		
Cage architecture		Osborne <i>et al.</i> , 2018
Chemical defense	Reduction of digestibility or increase of toxicity	Osborne <i>et al.</i> , 2018
Dispersal mode*		Chillo <i>et al.</i> , 2011
Digestible proteins*	Degree of attractiveness (proxy for palatability)	Chillo <i>et al.</i> , 2011
Leaf area*	Protection: reduces the size of the bite	Cornelissen <i>et al.</i> , 2003
Leaf phenology*		-
Maximum height*	Protection (avoidance)	Cornelissen <i>et al.</i> , 2003
Resprouting capacity*		Cornelissen <i>et al.</i> , 2003
Spinescence*	Protection: reduces the size of bite and the speed	Charles-Dominique <i>et al.</i> , 2016; Chillo <i>et al.</i> , 2011; Cornelissen <i>et al.</i> , 2003; Midgley <i>et al.</i> , 2016; Osborne <i>et al.</i> , 2018
Fire		
Bark thickness*	Tolerance: greater bark thickness for a given size class reduce topkill after fire	Lavorel and Garnier, 2002; Osborne <i>et al.</i> , 2018
Bud position in the bark	Buds protected by bark have greater survival after fire	Osborne <i>et al.</i> , 2018
Crown height	Resistance to disturbance through mechanical and architectural protection	Aubin <i>et al.</i> , 2016
Dispersal mode*	Recovery after disturbance	Aubin <i>et al.</i> , 2016
Leaf persistence*	Avoidance	Lavorel and Garnier, 2002
Mass of underground reserves	Tolerance	Lavorel and Garnier, 2002
Maximum height*	Avoidance	Lavorel and Garnier, 2002
Resprouting capacity*	Recovery after disturbance	Aubin <i>et al.</i> , 2016
Rooting depth	Tolerance	Lavorel and Garnier, 2002
Seed weight*	Recovery	Lavorel and Garnier, 2002; Ribeiro <i>et al.</i> , 2015
SLA*	Tolerance	Lavorel and Garnier, 2002

Table A13.1 – continued.

Response traits	Mechanisms	Sources
Drought		
Above ground biomass	Heat isolation	O'Brien <i>et al.</i> , 2017
Bark thickness*		Cornelissen <i>et al.</i> , 2003
Clonality (root sucker) *		Cornelissen <i>et al.</i> , 2003
Diameter at breast height		O'Brien <i>et al.</i> , 2017
Embolism resistance		O'Brien <i>et al.</i> , 2017
Growth form*		Cornelissen <i>et al.</i> , 2003
Height		O'Brien <i>et al.</i> , 2017
LDMC		Cornelissen <i>et al.</i> , 2003
Leaf area*		Cornelissen <i>et al.</i> , 2003
Leaf persistence*		Osborne <i>et al.</i> , 2018; Santiago <i>et al.</i> , 2016
Leaf phenology*	Avoidance of water loss	Cornelissen <i>et al.</i> , 2003
Potential conductivity		O'Brien <i>et al.</i> , 2017
Resprouting capacity*		Cornelissen <i>et al.</i> , 2003
Seed weight*		Cornelissen <i>et al.</i> , 2003
SLA*		Cornelissen <i>et al.</i> , 2003
Taproot*		Cornelissen <i>et al.</i> , 2003; O'Brien <i>et al.</i> , 2017; Osborne <i>et al.</i> , 2018; Poorter and Markesteijn, 2008
Vessel area*		O'Brien <i>et al.</i> , 2017
Wood density*		Craven <i>et al.</i> , 2016; Mouillot <i>et al.</i> , 2013; Osborne <i>et al.</i> , 2018; Poorter and Markesteijn, 2008

Table A13.2 – Literature sources (examples) linking effect traits to the two studied functions.

Function	Effect traits	Sources
Primary productivity	Growth form	-
	Maximum height	Mensah <i>et al.</i> , 2016
	Leaf area	de Bello <i>et al.</i> , 2010
	Specific leaf area	de Bello <i>et al.</i> , 2010; Mensah <i>et al.</i> , 2016
	Leaf N content	de Bello <i>et al.</i> , 2010
	Wood density	Mensah <i>et al.</i> , 2016
Biogeochemical cycles	Growth form	Cornelissen <i>et al.</i> , 2003
	Maximum height	Cornelissen <i>et al.</i> , 2003
	Leaf area	Cornelissen <i>et al.</i> , 2003
	Specific leaf area	Cornelissen <i>et al.</i> , 2003
	Leaf persistence	-
	Duration of leafing period	Cornelissen <i>et al.</i> , 2003
	Leaf N content	Cornelissen <i>et al.</i> , 2003
	Leaf P content	Cornelissen <i>et al.</i> , 2003
	N fixer	Cornelissen <i>et al.</i> , 2003
	Resprouting capacity	Cornelissen <i>et al.</i> , 2003
	Wood density	Cornelissen <i>et al.</i> , 2003

Appendix 14: Sources consulted for traits data compilation

A14.1. Traits searched in the TRY database

Table A14.1 – List of traits searched in the TRY database (Kattge *et al.*, 2011) and their number of identification.

Traits	Id trait in TRY
Whole plant traits	
Plant defense mechanism chemical	346
Plant defense mechanism physical	345
Plant growth form	42
Plant height	18
Plant lifespan (longevity)	59
Plant tolerance to drought	30
Plant tolerance to fire	318
Plant tolerance to grazing	228
Plant tolerance to human impact	199
Plant tolerance to shade	603
Plant tolerance to waterlogging	61
Plant nitrogen fixation capacity	8
Leaf traits	
Leaf area	1
Leaf dry matter content	47
Leaf lifespan	12
Leaf Nitrogen content per leaf dry mass	14
Leaf palatability	152
Leaf phenology type	37
Leaf Phosphorus content per leaf dry mass	15
Leaf texture	2
Leaf thickness	46
Specific leaf area	11
SLA based on fresh mass	125
Stem traits	
Bark thickness	24
Wood density	4
Belowground traits	
Fine root diameter	896
Plant mycorrhizal type	7
Root architecture type	65
Root length	1079
Rooting depth	6
Specific root length	1080

Table A14.1 – continued.

Traits	Id trait in TRY
Regenerative traits	
Dispersal distance	28
Dispersal syndrome	193
Dispersal unit dry mass	233
Plant propagation type	609
Plant resprouting capacity	819
Pollination syndrome	29
Seed dry mass	26
Seed longevity	33
Seed number per plant	131
Seedbank type	159

A14.2. Complete list of sources for the traits search beside TRY

Below is the complete list of sources that helped to complete the species-trait matrix. This is not the list of the source consulted; only the documents that actually allowed to fill the matrix are listed.

Height, growth form, spinescence: Arbonnier, 2009

Stem traits:

- Databases: Wheeler, 2011; Zanne *et al.*, 2009a; Zanne *et al.*, 2009b (Inside Wood, Global Vessel Database and Global Wood density database); Kindt *et al.*, 2013 (ICRAF database); Royal Botanic Gardens Kew, 1999 (Sepasal database); Wageningen University (Prota4u database);
- Others: Chiveu *et al.*, 2009; Hiernaux *et al.*, 1994; Robert and Björn, 2000; Van den Bilcke *et al.*, 2013.

Leaf traits : Ali *et al.*, 2007; Bille, 1977; Brandt *et al.*, 2016; Breman and De Ridder, 1991; Breman and Kessler, 1995; De Bie *et al.*, 1998; Diémé *et al.*, 2017; Fall, 1991; Farahat *et al.*, 2016; Grouzis and Le Floch, 2003; Hiernaux *et al.*, 1994; Kgope and Musil, 2004; Le Houérou, 1980a; Poupon, 1979; Poupon, 1980; Poupon and Bille, 1974; Seghieri *et al.*, 2012; Tezara *et al.*, 2011.

Belowground traits:

- Databases: Royal Botanic Gardens Kew, 1999 (SEPASAL database); Kindt *et al.*, 2013 (ICRAF database); Wageningen University (Prota4u database);

- Others: Baumer, 1983; Bille, 1977; Breman and Kessler, 1995; Breman and Sissoko, 1998; Clanet and Gillet, 1980; Diouf *et al.*, 2005; Gebrekirstos *et al.*, 2006; Guissou, 2001; Kizito *et al.*, 2006; Mayus *et al.*, 1998; Osborne *et al.*, 2018; Seghieri *et al.*, 2012; Tybirk, 1991.

Regenerative traits:

- Databases: Kew Garden: Royal Botanic Gardens Kew, 2008 (seed information database); Kindt *et al.*, 2013 (ICRAF database); Royal Botanic Gardens Kew, 1999 (SEPASAL database); Wageningen University (Prota4U database);
- Seed leaflets University of Copenhagen : Joker, 2000a; Joker, 2000b; Joker, 2000c; Joker, 2000d; Joker, 2003; Joker and Erdey, 2003; Sacande *et al.*, 2006; Sacande and Sanogo, 2007; Sacande *et al.*, 2007a; Sacande *et al.*, 2007b; Sanon *et al.*, 2007; Schmidt and Joker, 2000; Schmidt and Mbora, 2008a; Schmidt and Mbora, 2008b; Vautier *et al.*, 2007;
- Others: Abdourhamane *et al.*, 2017; Arbonnier, 2009; Bellefontaine, 1997; Clanet and Gillet, 1980; Colombo *et al.*, 2015; Danthu *et al.*, 1996; De Bie *et al.*, 1998; Dukku, 2010; Garner and Witkowski, 1997; Helm *et al.*, 2011; Kirchmair *et al.*, 2012; Lahoreau *et al.*, 2006; Midgley, 1998; Poupon, 1979; Schmidt *et al.*, 2013; Sen, 1968; Steentoft, 1988; Tréca and Tamba, 1997; Tybirk, 1991; Wilson and Witkowski, 1998.

Appendices to Chapter 4

Appendix 15: Species inventoried at the adult stage in 2015

Table A15.1 – Species inventoried at the adult stage in the 139 plots (N: number of adults), their mean dimensions and their standard deviation (sd).

Species	N	Mean height ± sd (m)	Mean circumference ± sd (cm)	Mean crown diameter ± sd (m)
<i>Acacia ataxacantha</i>	1	5.0	NA	7.9
<i>Acacia nilotica</i>	4	11.2 ± 4.1	93.3 ± 57.6	15.8 ± 1.2
<i>Acacia senegal</i>	23	5.3 ± 2.0	40.7 ± 23.3	6.1 ± 2.5
<i>Acacia seyal</i>	43	7.1 ± 2.6	54.7 ± 32.3	7.1 ± 2.7
<i>Acacia tortilis</i> subsp. <i>raddiana</i>	68	5.9 ± 3.3	56.9 ± 41.4	7.2 ± 4.1
<i>Adansonia digitata</i>	6	14.1 ± 3.7	608.3 ± 251.1	12.9 ± 3.2
<i>Adenium obesum</i>	1	4.6	250.0	2.9
<i>Anogeissus leiocarpa</i>	2	14.0 ± 1.3	326.5 ± 23.3	17.0 ± 0.7
<i>Balanites aegyptiaca</i>	688	5.7 ± 2.7	56.0 ± 36.0	4.6 ± 2.5
<i>Bauhinia rufescens</i>	1	4.0	70.0	9.9
<i>Boscia senegalensis</i>	1169	1.5 ± 0.6	39.2 ± 27.8	1.9 ± 0.8
<i>Calotropis procera</i>	324	2.0 ± 1.2	72.7 ± 40.0	1.7 ± 0.9
<i>Combretum aculeatum</i>	1	4.1	95.0	6.2
<i>Combretum glutinosum</i>	21	7.6 ± 2.7	81.8 ± 53.4	7.0 ± 2.5
<i>Commiphora africana</i>	2	3.5 ± 0.7	33.0 ± 19.8	4.6 ± 0.4
<i>Dalbergia melanoxylon</i>	1	5.7	165.0	5.0
<i>Faidherbia albida</i>	1	15.3	147.0	12.4
<i>Feretia apodanthera</i>	4	3.4 ± 1.1	45.3 ± 20.8	2.9 ± 1.4
<i>Grewia bicolor</i>	51	4.6 ± 1.3	86.0 ± 38.7	5.5 ± 1.5
<i>Guiera senegalensis</i>	26	4.1 ± 1.1	69.7 ± 41.4	5.3 ± 2.0
<i>Leptadenia pyrotechnica</i>	9	2.1 ± 0.3	163.9 ± 96.5	2.7 ± 1.1
<i>Sclerocarya birrea</i>	104	9.2 ± 2.4	113.5 ± 44.0	9.6 ± 2.5
<i>Stereospermum kunthianum</i>	2	12.5 ± 1.5	170.5 ± 101.1	10.2 ± 4.1
<i>Ziziphus mauritiana</i>	10	6.0 ± 2.5	114.7 ± 67.3	8.7 ± 3.8

Appendix 16: Features of the nearest adults from seedlings

Table A16.1 – Mean dimensions of the adults located the nearest from the seedlings, per seedlings species. The number of seedlings counted on the 70 sub-sampled plots is indicated between brackets.

Species of seedlings	Mean dimensions of the nearest adults		
	Circumference (cm)	Height (m)	Crown diameter (m)
<i>Acacia nilotica</i> (2)	73.0	5.5	7.0
<i>Acacia senegal</i> (11)	73.2	3.2	3.5
<i>Acacia seyal</i> (453)	54.4	7.6	5.5
<i>Acacia tortilis</i> (44)	124.6	3.1	3.2
<i>Adansonia digitata</i> (25)	87.4	5.4	5.6
<i>Balanites aegyptiaca</i> (645)	72.3	6.1	4.8
<i>Bauhinia rufescens</i> (11)	43.0	1.6	1.9
<i>Combretum aculeatum</i> (7)	32.0	2.0	1.8
<i>Combretum glutinosum</i> (1)	62.0	7.0	4.1
<i>Commiphora africana</i> (1)	65.0	1.8	2.4
<i>Feretia apodanthera</i> (2)	178.0	9.5	10.7
<i>Grewia bicolor</i> (123)	90.9	5.4	5.7
<i>Guiera senegalensis</i> (42)	51.2	4.2	8.1
<i>Sclerocarya birrea</i> (211)	130.6	9.5	10.4
<i>Stereospermum kunthianum</i> (1)	23.0	1.6	0.8
<i>Ziziphus mauritiana</i> (47)	112.8	6.1	7.5

Appendices to Chapter 5

Appendix 17: Results of the linear mixed models

Table A17.1 – Results of the linear mixed models applied to study woody cover and density changes.

Mixed models for density changes				
Response variable and simplified equations	Fixed effect parameters	Estimates	SE	p
Density: density ~ year + type + (1 site)	Intercept	15.49	0.98	< 0.001
	year.2008	-2.15	0.22	< 0.001
	year.2018	-0.92	0.22	< 0.001
	type.dune	-5.01	1.32	< 0.01
	type.plain	1.98	1.32	ns
Delta density 2008-1980: delta.d08.80 ~ type + (1 site)	Intercept	-0.49	1.11	ns
	type.dune	-2.5	1.5	ns
	type.plain	-2.18	1.5	ns
Delta density 2018-2008: delta.d18.08 ~ type + (1 site)	Intercept	2.29	1.07	0.05
	type.dune	-1.44	1.45	ns
	type.plain	-1.58	1.45	ns
Delta density 2018-1980: delta.d18.80 ~ type + (1 site)	Intercept	1.8	1.43	ns
	type.dune	-3.95	1.94	ns
	type.plain	-3.76	1.94	ns
Mixed models for woody cover changes				
Response variable and simplified equations	Fixed effect parameters	Estimates	SE	p
Woody cover: woody.cover ~ year + type + (1 site)	Intercept	3.06	0.45	< 0.001
	year.2008	-0.61	0.15	< 0.001
	type.dune	-0.19	0.61	ns
	type.plain	2.75	0.61	< 0.001
Delta woody cover: delta.WC ~ type + (1 site)	Intercept	-0.34	0.69	ns
	type.dune	0.56	0.94	ns
	type.plain	-1.32	0.94	ns

Appendix 18: Validation of the classification with 100 points per site

Table A18.1 – Validation points randomly distributed between the classes “tree” and “no tree” to validate the thresholds applied on aerial photos and on WorldView-1.

	Aerial photo thresholds		
	N	Total N of points	Ratio (%)
Tree points <i>correctly</i> classified as “tree”	138	170	81.2
Tree points <i>wrongly</i> classified as “tree”	32	170	18.8
No tree points <i>correctly</i> classified as “no tree”	1490	1530	97.4
No tree points <i>wrongly</i> classified as “no tree”	40	1530	2.6

	WorldView thresholds		
	N	Total N of points	Ratio (%)
Tree points <i>correctly</i> classified as “tree”	154	170	90.6
Tree points <i>wrongly</i> classified as “tree”	16	170	9.4
No tree points <i>correctly</i> classified as “no tree”	1506	1530	98.4
No tree points <i>wrongly</i> classified as “no tree”	24	1530	1.6

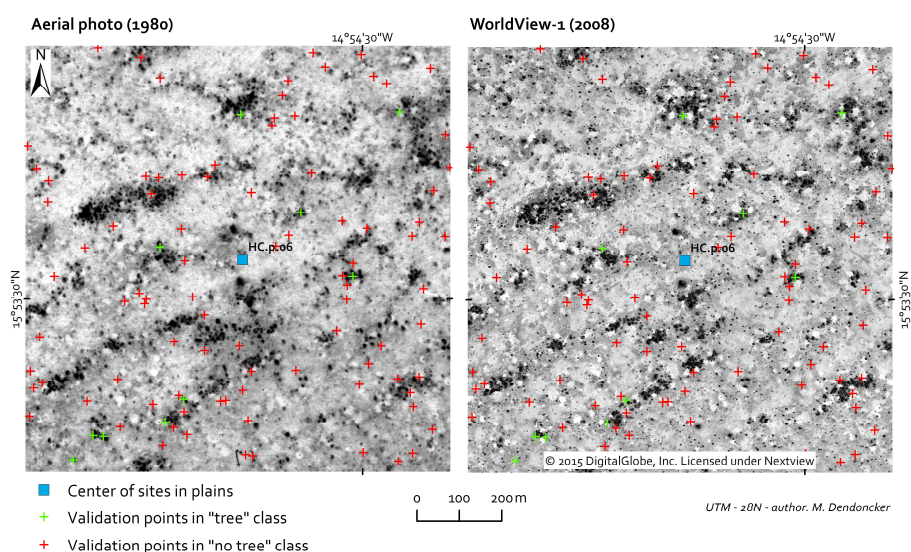


Figure A18.1 – Example of distribution of the validation points for a site in plain (HC.p.06) on aerial photo (left) and on WorldView-1 (right).

Appendix 19: Evolution of woody cover on the 17 sites of 1 km²

The square indicates the center of the study site. The red areas indicate trees canopies that have disappeared between 1980 and 2008 whereas the green areas point to canopies that have appeared during the same time. Blue areas show unchanged tree canopies.

Panels (a) show aerial photos from 1980; panels (b) show WorldView-1 images from 2008 and panels (c) show WorldView-1 with woody cover changes highlighted.

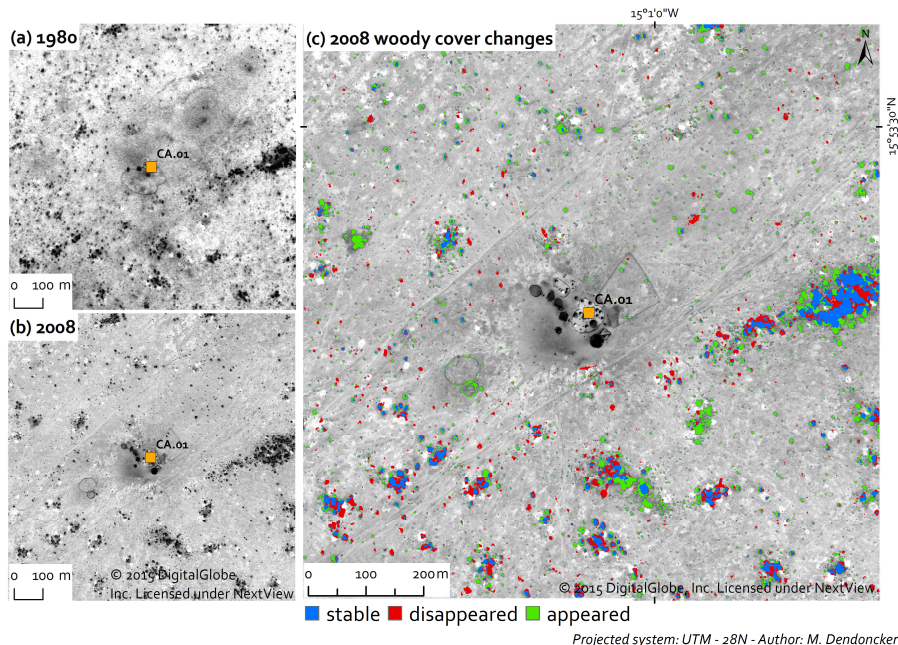


Figure A19.1 – Changes in woody cover for the 17 sites. (a) Woody cover in 1980; (b) woody cover in 2008; (c) highlights of the stable, disappeared and appeared trees.

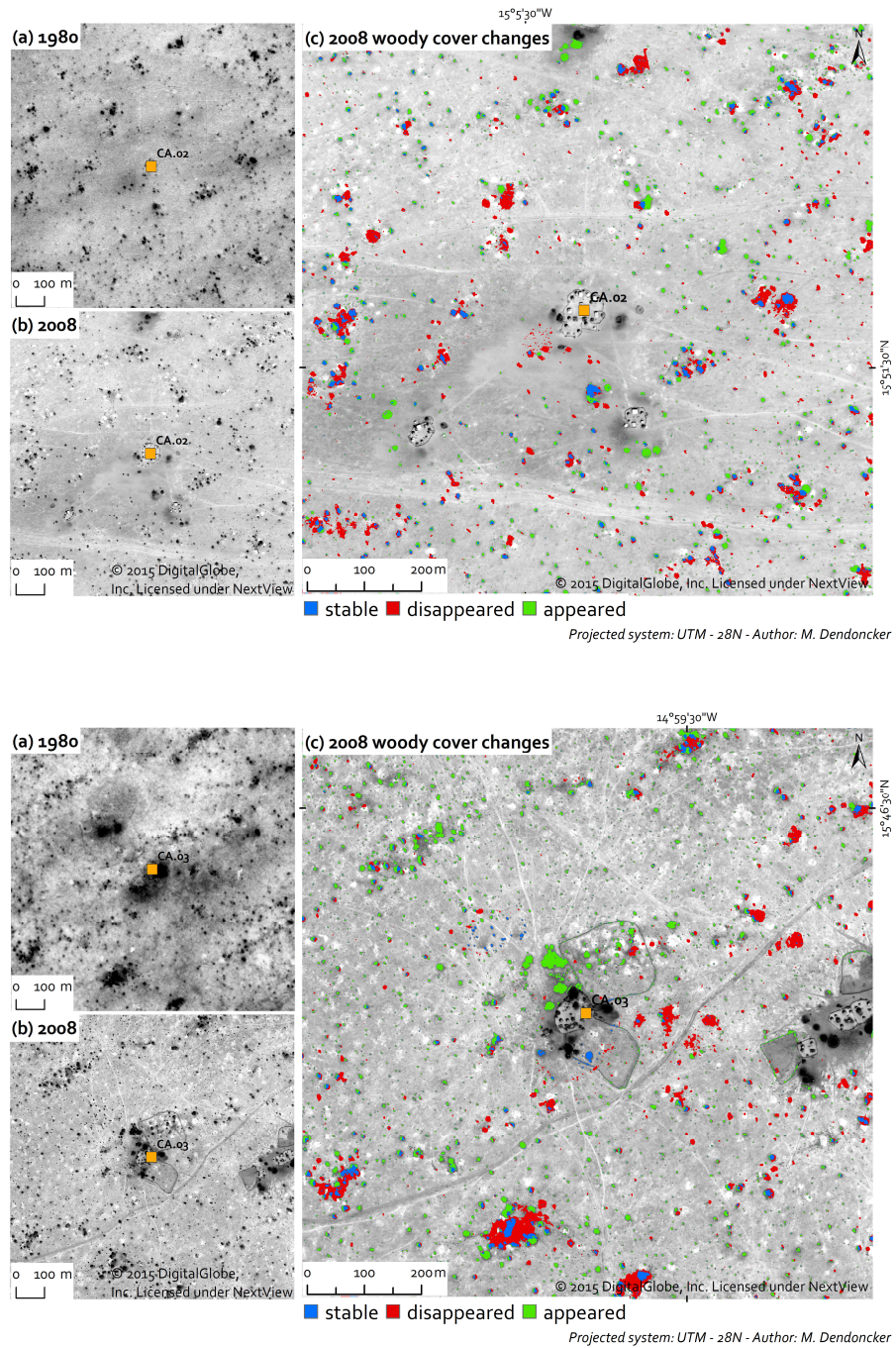


Figure A19.1 – continued.

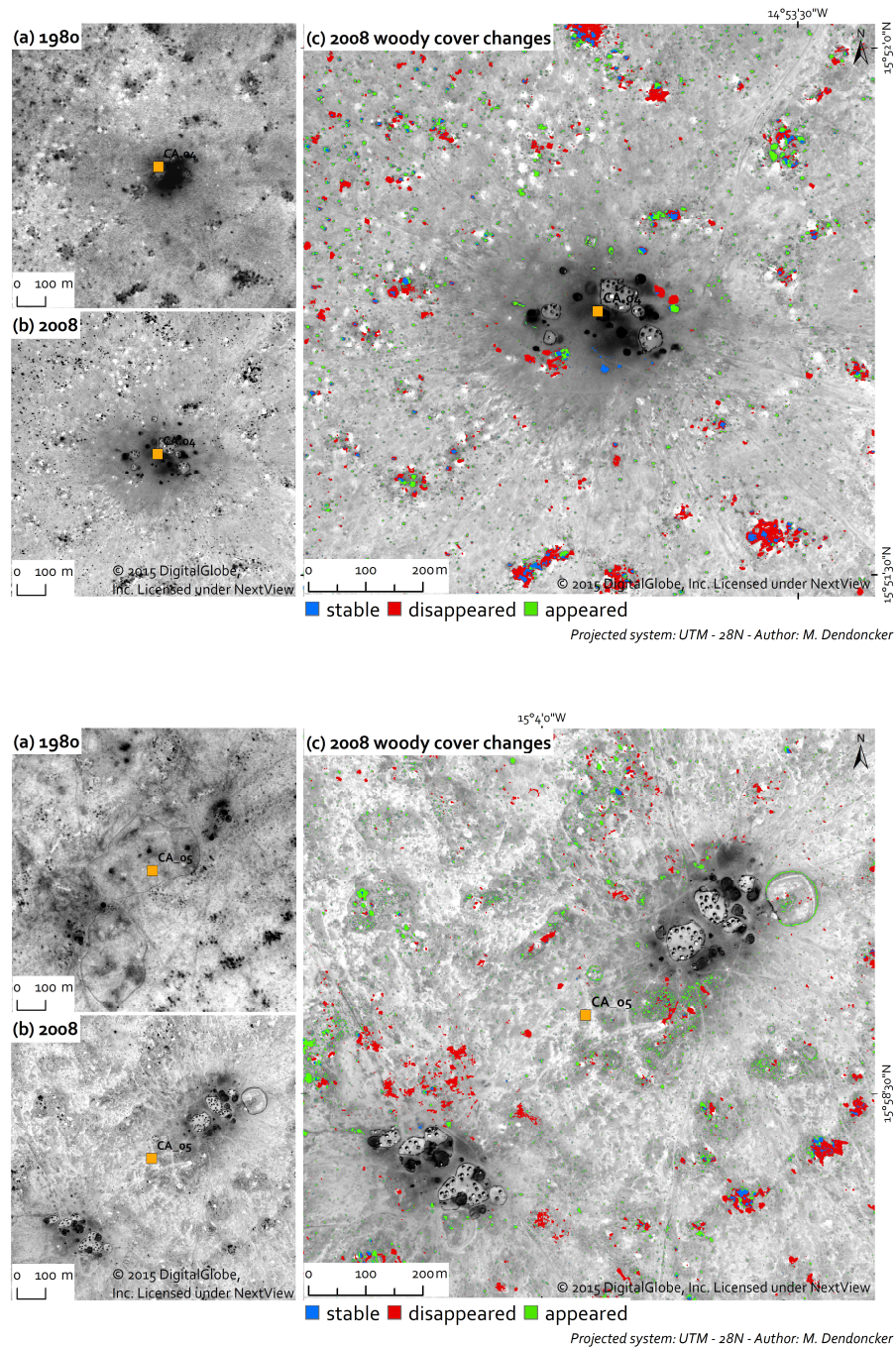


Figure A19.1 – continued.

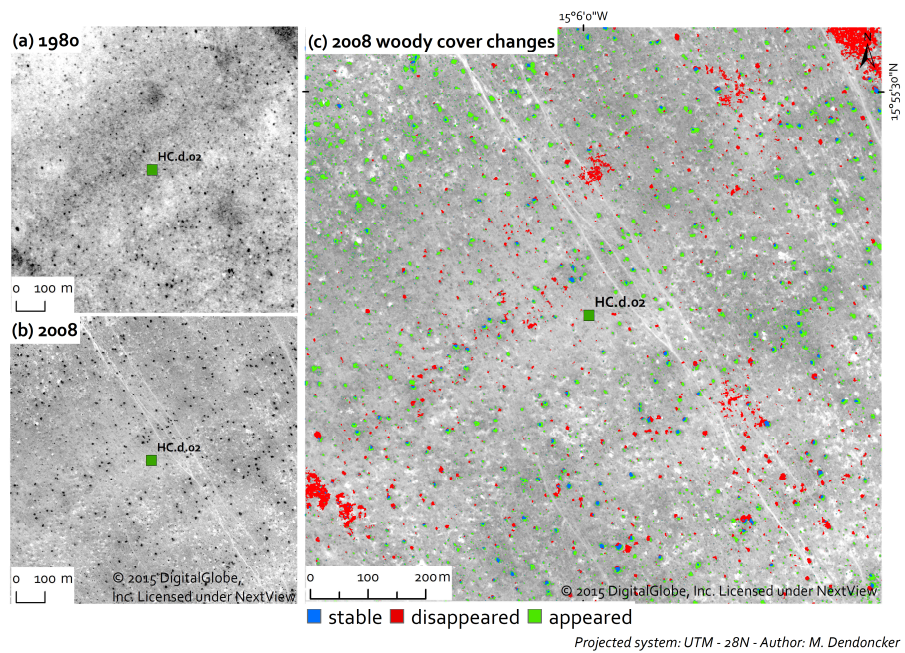
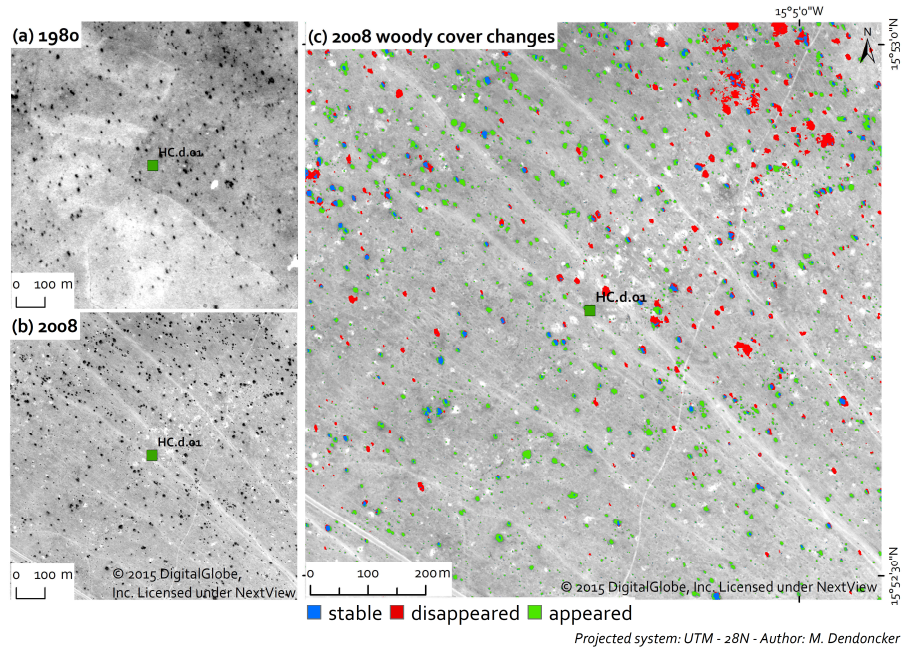


Figure A19.1 – continued.

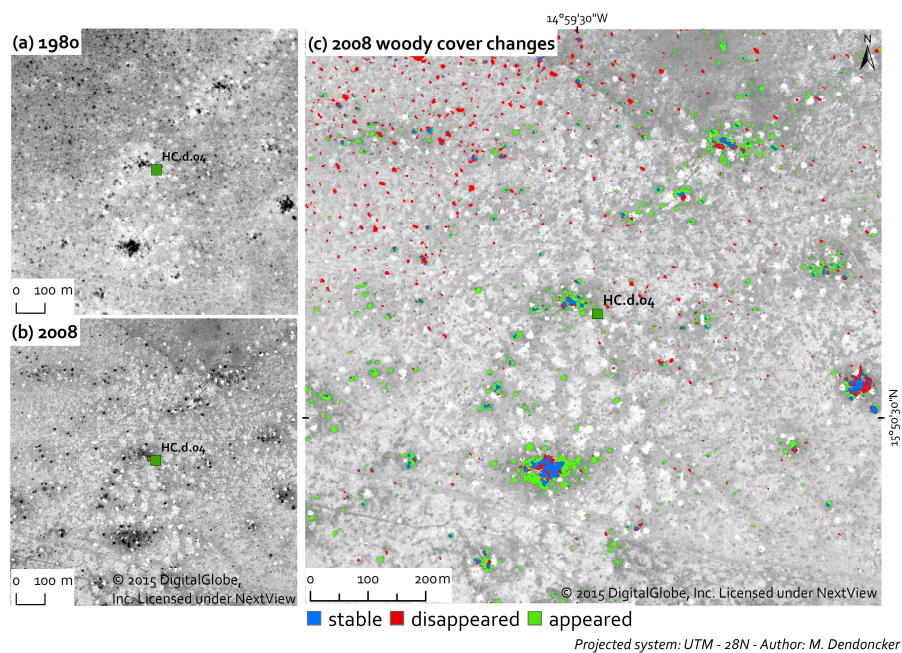
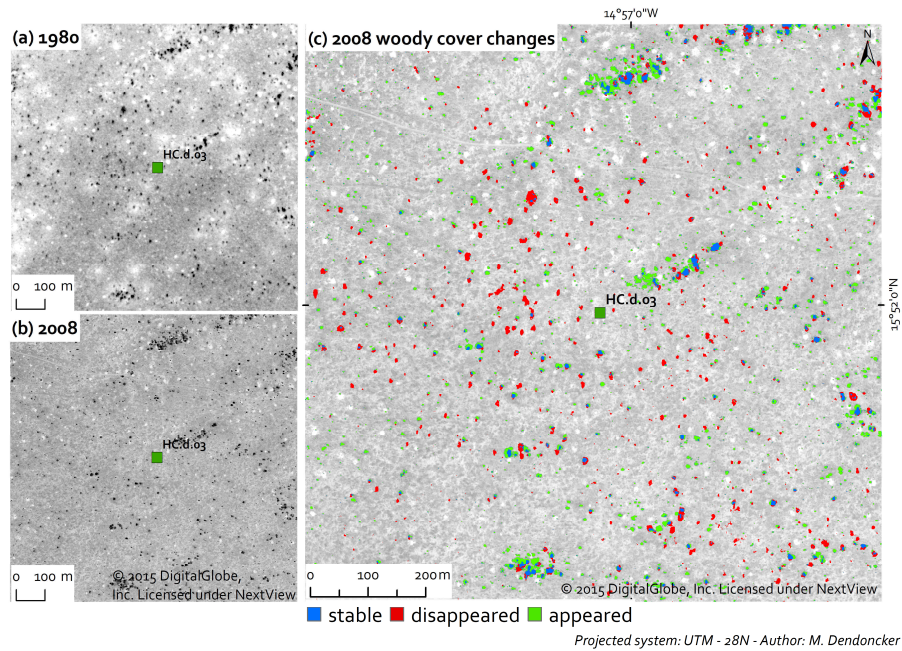


Figure A19.1 – continued.

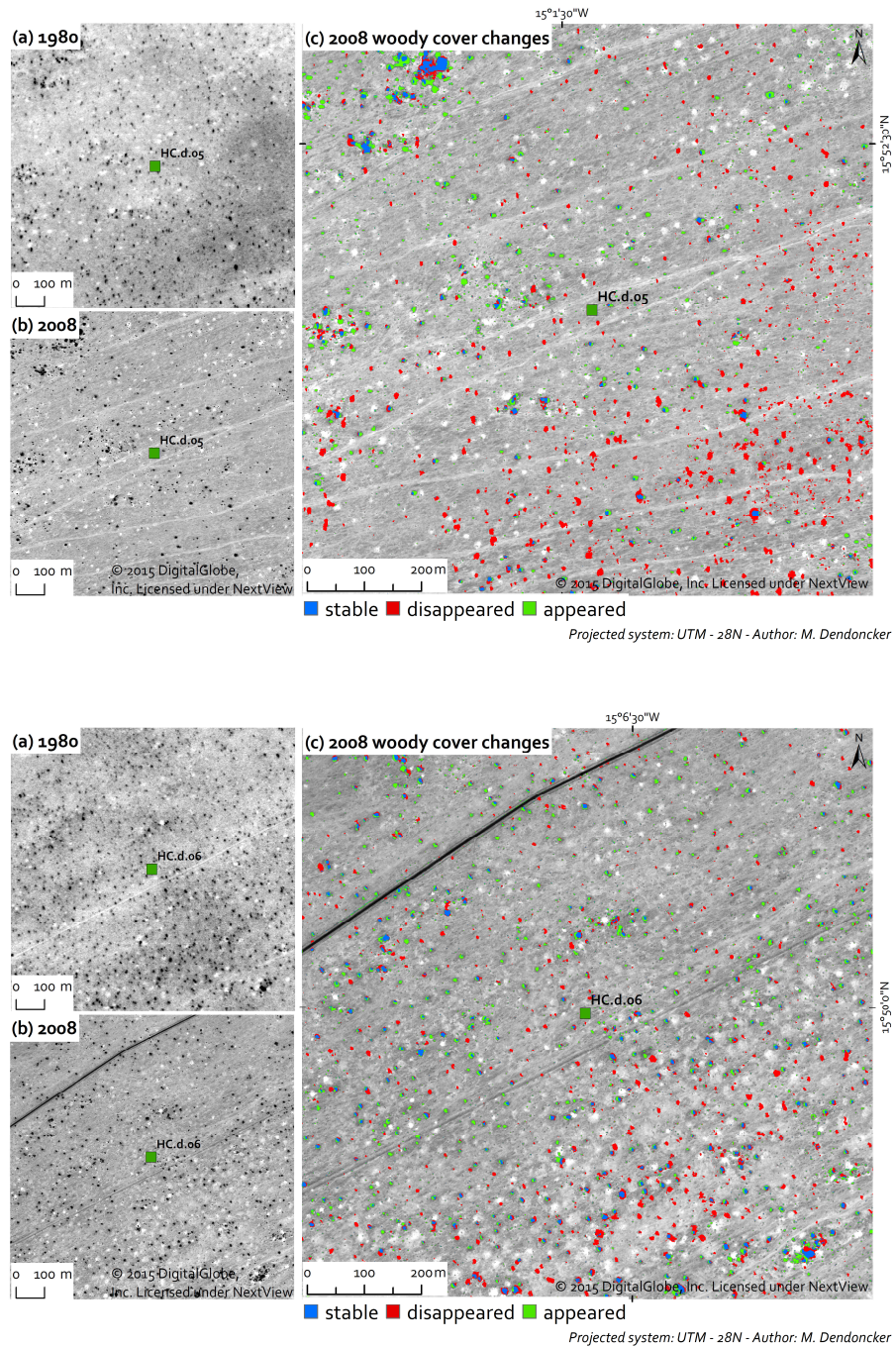


Figure A19.1 – continued.

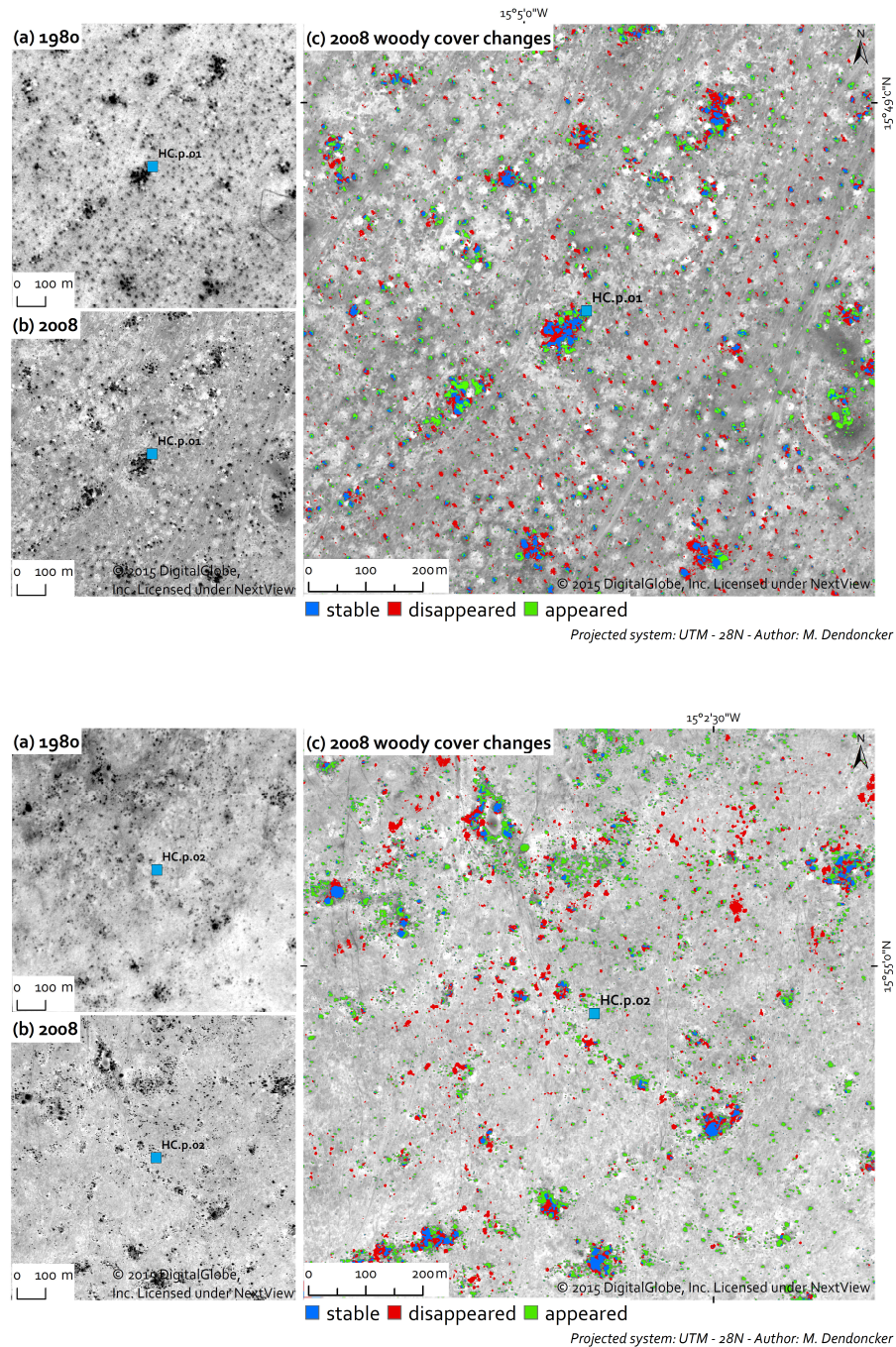


Figure A19.1 – continued.

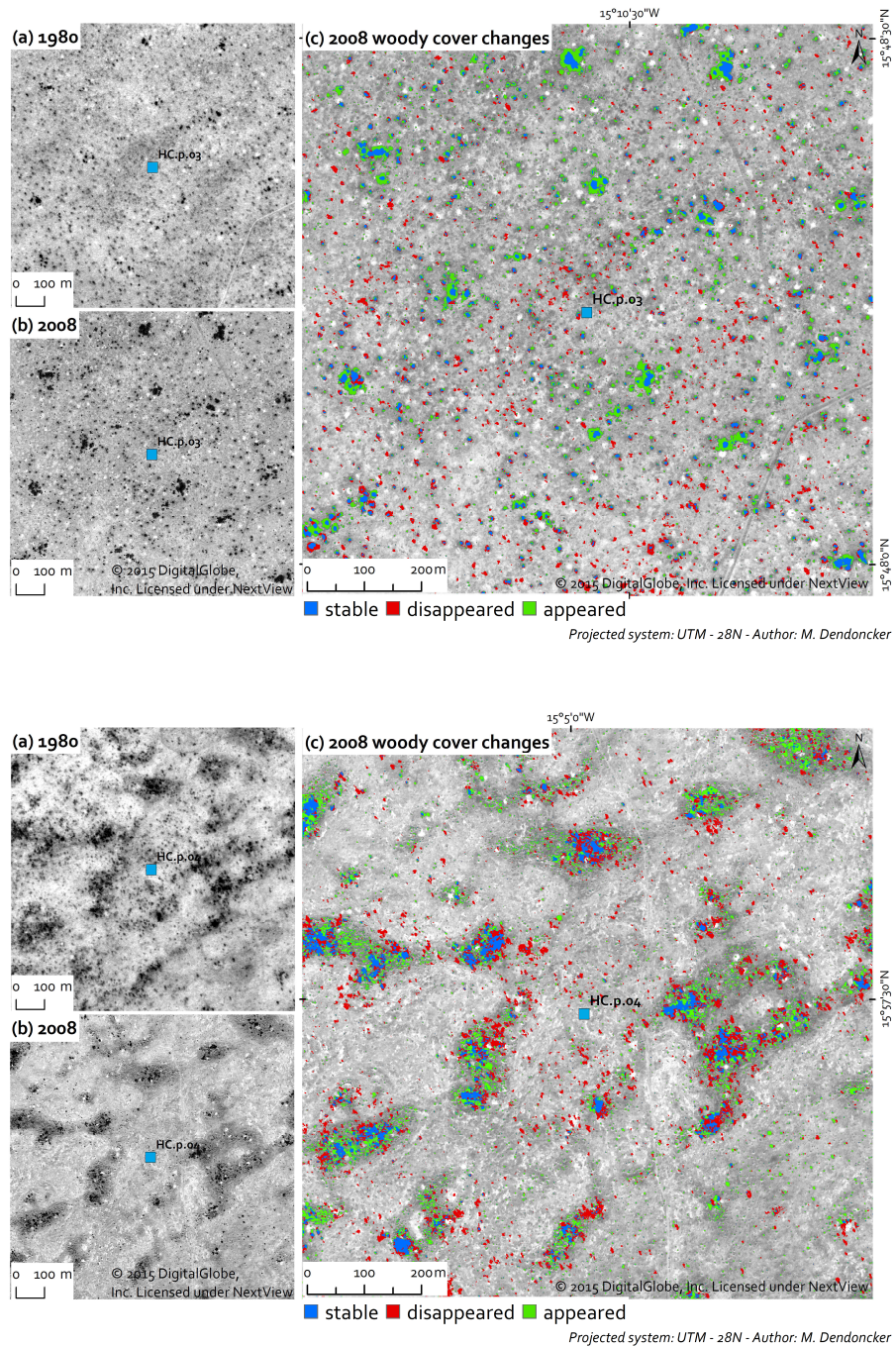


Figure A19.1 – continued.

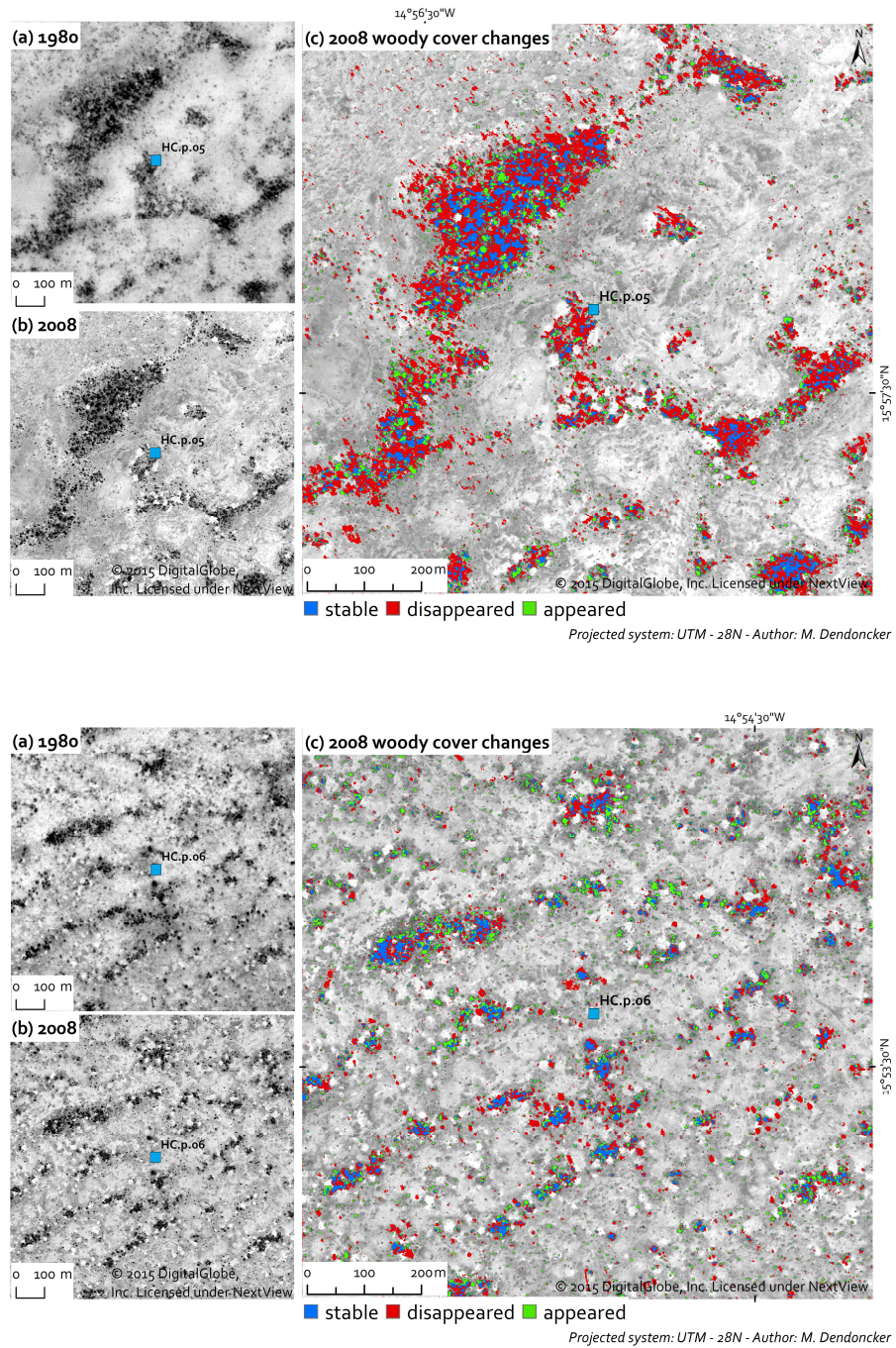


Figure A19.1 – continued.

Appendix 20: Species inventoried in 2017

Table A20.1 – Species recorded during fieldwork of December 2017, their frequency and their presence on the two relief elements.

Species	Frequency (%)	Dunes	Plains
<i>Acacia nilotica</i>	3.3	-	+
<i>Acacia senegal</i>	16.7	+	+
<i>Acacia seyal</i>	3.3	-	+
<i>Acacia tortilis</i>	10.0	+	+
<i>Adansonia digitata</i>	3.3	+	-
<i>Balanites aegyptiaca</i>	33.3	+	+
<i>Boscia senegalensis</i>	96.7	+	+
<i>Calotropis procera</i>	20.0	+	+
<i>Combretum glutinosum</i>	10.0	+	-
<i>Feretia apodanthera</i>	3.3	-	+
<i>Grewia bicolor</i>	3.3	-	+
<i>Guiera senegalensis</i>	10.0	+	+
<i>Leptadenia pyrotechnica</i>	16.7	+	+
<i>Sclerocarya birrea</i>	33.3	+	+
<i>Stereospermum kunthianum</i>	3.3	-	+
<i>Terminalia avicennioides</i>	3.3	-	+
<i>Ziziphus mauritiana</i>	3.3	-	+

Species recorded in the subset of the Flotrop database

Table A20.2 – Change in relative frequency for the species recorded in the subset of the Flotrop database and in the field inventory of 2015-2017.

Species	Flotrop frequency (%)	Field inventory 2015-2017 frequency (%)	Relative change frequency
<i>Acacia ataxacantha</i>	0.36	0.59	63.53
<i>Acacia erythrocalyx</i>	0.36	0	-100
<i>Acacia macrostachya</i>	1.08	0	-100
<i>Acacia nilotica</i>	0	2.35	NA
<i>Acacia senegal</i>	26.98	10.59	-60.75
<i>Acacia seyal</i>	14.39	7.65	-46.85
<i>Acacia tortilis</i> subsp. <i>raddiana</i>	5.76	22.35	288.38
<i>Adansonia digitata</i>	4.32	4.71	9.02
<i>Adenium obesum</i>	3.24	0.59	-81.83
<i>Anogeissus leiocarpa</i>	1.44	1.18	-18.24
<i>Balanites aegyptiaca</i>	65.83	56.47	-14.21
<i>Bauhinia rufescens</i>	0.72	0.59	-18.24
<i>Boscia senegalensis</i>	66.55	75.88	14.03
<i>Bridelia ferruginea</i>	0.36	0	-100
<i>Calotropis procera</i>	25.54	27.06	5.95
<i>Combretum aculeatum</i>	21.94	0.59	-97.32
<i>Combretum glutinosum</i>	38.49	11.76	-69.43
<i>Commiphora africana</i>	30.22	1.18	-96.11
<i>Cordia sinensis</i>	0.36	0	-100
<i>Dalbergia melanoxylon</i>	2.52	1.18	-53.28
<i>Dichrostachys cinerea</i>	3.96	0	-100
<i>Entada africana</i>	0.36	0	-100
<i>Faidherbia albida</i>	0.72	0.59	-18.24
<i>Feretia apodanthera</i>	2.16	2.94	36.27
<i>Grewia bicolor</i>	24.46	14.71	-39.88
<i>Grewia flavescens</i>	0.36	0	-100
<i>Guiera senegalensis</i>	55.4	7.06	-87.26
<i>Lannea acida</i>	0.72	0	-100
<i>Leptadenia hastata</i>	12.23	19.41	58.72
<i>Leptadenia pyrotechnica</i>	6.47	7.65	18.1
<i>Maerua angolensis</i>	2.16	0	-100
<i>Maytenus senegalensis</i>	0.36	0	-100
<i>Mitragyna inermis</i>	1.08	0	-100
<i>Piliostigma reticulatum</i>	0.36	0	-100
<i>Sclerocarya birrea</i>	78.06	40.59	-48
<i>Sterculia setigera</i>	8.63	0	-100
<i>Stereospermum kunthianum</i>	0.36	1.18	227.06
<i>Syzygium guineense</i>	0.36	0	-100
<i>Terminalia avicennioides</i>	4.32	0.59	-86.37
<i>Ziziphus mauritiana</i>	4.32	4.12	-4.61

Appendix 21: Species composition per climatic period

The following table gathers the species that are recorded in the subset of the Flotrop database (as described in section 3.3.2) and the ones recorded during our field inventory (at the adult phase). This list does not represent with certainty the whole species composition per period. Indeed, rare species may have been overlooked due to the sampling design, which is unknown for Flotrop. As an example, an individual of *Maerua angolensis*, *Sterculia setigera*, *Maerua crassifolia* and *Capparis tomentosa* have been observed outside our plots in 2015.

Table A21.1 – Species list for to three climatic periods (before, during and after the great drought).

Source	Flotrop	Flotrop	Field inventory
Period	1965-1971	1972-1997	2015-2017
Number of surveys or plots	80	198	139+30
<i>Acacia ataxacantha</i>		+	+
<i>Acacia erythrocalyx</i>	+		
<i>Acacia macrostachya</i>		+	
<i>Acacia senegal</i>	+	+	+
<i>Acacia seyal</i>	+	+	+
<i>Acacia tortilis</i>	+	+	+
<i>Adansonia digitata</i>	+	+	+
<i>Adenium obesum</i>	+	+	+
<i>Anogeissus leiocarpa</i>	+	+	+
<i>Balanites aegyptiaca</i>	+	+	+
<i>Bauhinia rufescens</i>	+		+
<i>Boscia senegalensis</i>	+	+	+
<i>Bridelia ferruginea</i>		+	
<i>Calotropis procera</i>	+	+	+
<i>Combretum aculeatum</i>	+	+	+
<i>Combretum glutinosum</i>	+	+	+
<i>Commiphora africana</i>	+	+	+
<i>Cordia sinensis</i>		+	
<i>Dalbergia melanoxylon</i>	+	+	+
<i>Dichrostachys cinerea</i>		+	
<i>Euphorbia balsamifera*</i>	+		
<i>Entada africana</i>		+	
<i>Faidherbia albida</i>		+	+
<i>Feretia apodanthera</i>	+	+	+
<i>Grewia bicolor</i>	+	+	+
<i>Grewia flavescens</i>	+		
<i>Guiera senegalensis</i>	+	+	+
<i>Lannea acida</i>	+		
<i>Leptadenia hastata</i>	+	+	+
<i>Leptadenia pyrotechnica</i>	+	+	+
<i>Maerna angolensis</i>		+	
<i>Mitragyna inermis</i>		+	
<i>Maytenus senegalensis</i>	+		
<i>Piliostigma reticulatum</i>	+		
<i>Sclerocarya birrea</i>	+	+	+
<i>Sterculia setigera</i>	+	+	
<i>Stereospermum kunthianum</i>	+		+
<i>Syzgium guineense</i>		+	
<i>Terminalia avicennioides</i>	+	+	+
<i>Ziziphus mauritiana</i>	+	+	+

* Not included in our analyses as this species is planted to create living hedges.

Appendices to Chapter 6

Appendix 22: The dissimilarity function

Extracted from Taugourdeau *et al.*, 2014

“The dissimilarity imputation method is based on the functional proximity between species. This method relies on the hypothesis that species with the same functional strategy have a similar set of functional traits (Diaz *et al.*, 2004; Westoby *et al.*, 2002). To replace the missing data of the trait T_j of the species S_i , the Gower dissimilarity (Gower 1971) between S_i and the other species is calculated based on the other traits. The species showing high similarity with S_i are then selected, and the median of their trait values for T_j is computed and used to evaluate the missing value T_{ji} . We chose a Gower dissimilarity coefficient of 0.05 as threshold for species with high similarity. The Gower dissimilarity can be computed with missing data, so the presence of other missing data would not disrupt replacement of the missing data.”

Appendix 23: Principal component analysis on species traits

The Principal Component Analysis discriminates which continuous traits differentiate the most the species. The first three axes explain 22.8, 20.8 and 12.7% of the total variability, respectively. The first axis mostly represents the variability of leaf nitrogen content (25.9%), wood density (18.6%) and seed weight (18.8%). The second axis expresses the variability of vessel area (33.1%) followed by the length of the fruits (24%). SLA and the maximum height are the main components of the third axis (37.4 and 32.3%).

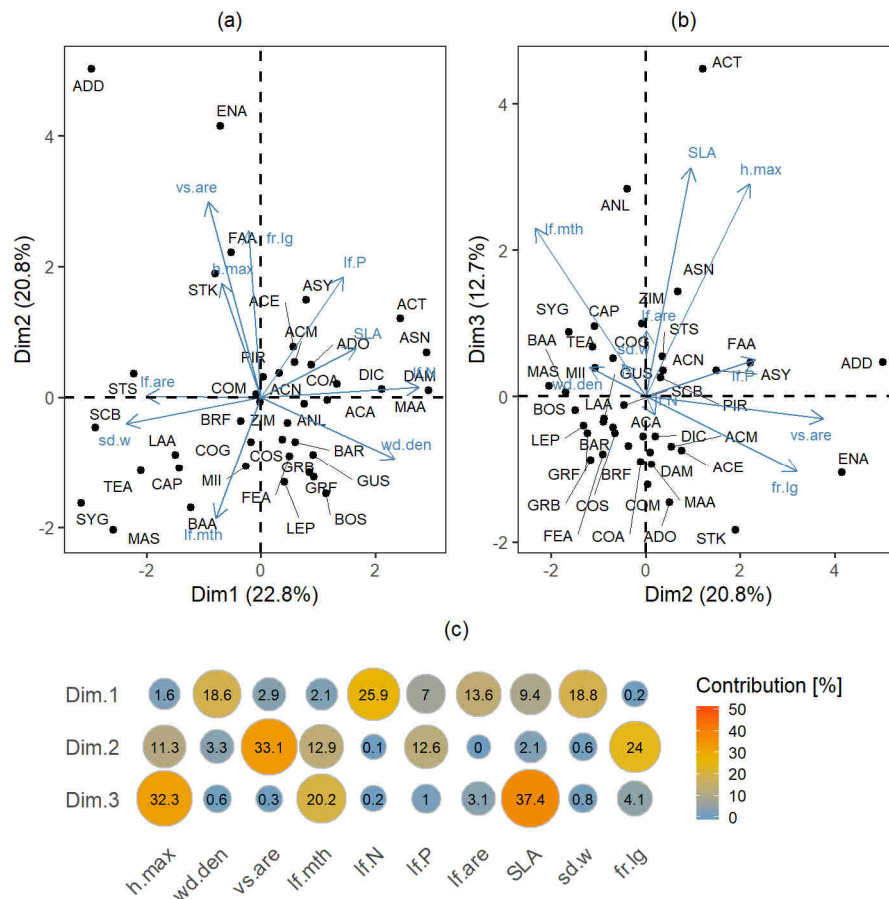


Figure A23.1 – Principal Component Analysis (a) biplot (traits and species) in the plane determined by dimension 1 and 2, (b) biplot in the plane determined by dimensions 2 and 3, (c) contribution (%) of the variables to the first three dimensions.

On the plane determined by axes 1 and 2, the species *Adansonia digitata* and *Entada africana* stand out, as they are remote from the other species. Table 6.5 indicates that these two species have the longest fruits (with *Stereospermum kunthianum*) of more than 30 cm and *Adansonia digitata* has the smallest wood density with 0.3 g cm^{-3} , two features that are quite different from the other species and are likely the cause of their positions in the PCA. We note that, while *Adansonia* is still present in the study area, *Entada* is among the rare species of Flotrop and was not recorded in 2015. On the plane of axis 2-3, *Adansonia* and *Entada* are still isolated by axis 2 but so is *Acacia tortilis* by axis 3, probably given his high SLA ($50 \text{ mm}^2.\text{mg}^{-1}$, Table 6.5).

Appendix 24: Temporal changes in functional diversity

Table A24.1 - Mean and standard deviation of CWM per period: maximum height (h.max), duration of leafing period (lf.mth), specific leaf area (SLA), leaf area (lf.are), seed weight (sd.w), fruit length (fr.lg), wood density (wd.den), vessel area (vs.are), leaf N content (lf.N) and leaf P content (lf.P). The number of plots is between brackets.

Different upper letters in a row indicate significant difference between periods ($P < 0.05$).

CWM	Before the great drought ($n = 78$)	During the great drought ($n = 49$)	After the great drought ($n = 139$)
h.max (m)	10.0 ± 2.1^b	10.1 ± 1.5^b	8.1 ± 2.9^a
lf.mth (months)	9.1 ± 1.9^a	9.4 ± 1.7^a	11.2 ± 1.0^b
SLA ($\text{mm}^2.\text{mg}^{-1}$)	5.26 ± 1.68^a	5.13 ± 1.79^a	9.49 ± 6.21^b
lf.are (mm^2)	2026.0 ± 1120.91^a	2118.24 ± 780.69^a	2556.63 ± 2924.59^b
sd.w (mg)	1165.51 ± 677.04^b	1246.73 ± 570.25^b	660.29 ± 408.67^a
fr.lg (mm)	39.0 ± 19.06^a	34.37 ± 7.95^a	42.68 ± 26.25^a
wd.den ($\text{g}.\text{cm}^{-3}$)	0.633 ± 0.085^a	0.646 ± 0.068^a	0.677 ± 0.040^b
vs.are (mm^2)	0.0105 ± 0.0020^b	0.0102 ± 0.0010^b	0.0094 ± 0.0027^a
lf.N ($\text{mg}.\text{g}^{-1}$)	21.83 ± 3.54^a	21.56 ± 3.35^a	28.61 ± 4.83^b
lf.P ($\text{mg}.\text{g}^{-1}$)	1.55 ± 0.25^b	1.52 ± 0.18^b	1.44 ± 0.21^a

Table A24.2 – Response diversity (means $\pm$ standard deviations of FDis) to the three responses for each functional group per period. The number of plots is between brackets. Different upper letters in a row indicate significant difference between periods ($P < 0.05$).

Response	FG	Before the great drought ($n = 78$)	During the great drought ($n = 78$)	After the great drought ($n = 139$)
Primary productivity				
Drought	FG-pp1	0.94 ± 0.58^b	0.50 ± 0.63^a	0.37 ± 0.57^a
	FG-pp2	1.20 ± 0.50^c	1.05 ± 0.48^b	0.60 ± 0.62^a
Fire	FG-pp1	0.90 ± 0.55^a	0.65 ± 0.71^a	0.67 ± 0.77^a
	FG-pp2	0.76 ± 0.45^b	0.79 ± 0.48^b	0.31 ± 0.39^a
Grazing	FG-pp1	0.78 ± 0.48^b	0.47 ± 0.49^a	0.50 ± 0.61^a
	FG-pp2	0.84 ± 0.40^b	0.78 ± 0.35^b	0.39 ± 0.43^a
Biogeochemical cycles				
Drought	FG-bc1	0.35 ± 0.44^b	0.04 ± 0.17^a	0.06 ± 0.25^a
	FG-bc2	0.40 ± 0.65^b	0.14 ± 0.41^a	0.07 ± 0.31^a
	FG-bc3	1.13 ± 0.52^b	0.85 ± 0.54^a	0.75 ± 0.60^a
Fire	FG-bc1	0.51 ± 0.63^b	0.07 ± 0.29^a	0.05 ± 0.21^a
	FG-bc2	0.26 ± 0.43^b	0.09 ± 0.28^a	0.06 ± 0.23^a
	FG-bc3	0.87 ± 0.42^a	0.82 ± 0.45^a	0.66 ± 0.53^a
Grazing	FG-bc1	0.40 ± 0.54^b	0.06 ± 0.26^a	0.04 ± 0.20^a
	FG-bc2	0.22 ± 0.40^b	0.06 ± 0.17^a	0.03 ± 0.13^a
	FG-bc3	0.97 ± 0.43^a	0.92 ± 0.51^a	0.82 ± 0.60^a

Appendix 25: Functional diversity in 2015

Table A25.1 – Functional diversity indices (means $\pm$ standard deviations) per topographic element ($n = 80$ plots, 39 depressions, 41 tops). Different upper letters in a row indicate significant difference between tops and depressions ($P < 0.05$).

Set of trait	FD indices	Depressions	Tops
Effect on primary productivity	FRic	0.356 ± 0.200^b	0.235 ± 0.193^a
	FEve	0.645 ± 0.229^a	0.748 ± 0.171^b
	FDiv	0.825 ± 0.149^a	0.843 ± 0.118^a
	FDis	0.137 ± 0.068^a	0.132 ± 0.081^a
Effect on biogeochemical cycles	FRic	0.311 ± 0.226^b	0.148 ± 0.134^a
	FEve	0.594 ± 0.237^a	0.702 ± 0.194^a
	FDiv	0.852 ± 0.130^a	0.789 ± 0.142^a
	FDis	0.114 ± 0.052^a	0.114 ± 0.072^a
Response to drought	FRic	0.407 ± 0.267^b	0.238 ± 0.195^a
	FEve	0.632 ± 0.211^a	0.735 ± 0.168^a
	FDiv	0.815 ± 0.158^a	0.806 ± 0.111^a
	FDis	0.132 ± 0.058^a	0.133 ± 0.080^b
Response to fire	FRic	0.320 ± 0.202^a	0.230 ± 0.206^a
	FEve	0.625 ± 0.219^a	0.705 ± 0.204^a
	FDiv	0.854 ± 0.139^a	0.874 ± 0.109^a
	FDis	0.103 ± 0.048^a	0.112 ± 0.068^b
Response to grazing	FRic	0.242 ± 0.130^b	0.120 ± 0.103^a
	FEve	0.591 ± 0.206^a	0.791 ± 0.170^b
	FDiv	0.743 ± 0.197^a	0.715 ± 0.156^a
	FDis	0.105 ± 0.058^a	0.089 ± 0.066^a

Table A25.2 – CWM (means $\pm$ standard deviations) per topographic element ($n = 139$ plots, 43 depressions, 96 tops). Different upper letters in a row indicate significant difference between tops and depressions ($P < 0.05$).

CWM	Depressions	Tops
Maximum height (m)	7.8 ± 2.0^a	8.3 ± 3.3^a
Duration of leafing period (months)	11.4 ± 0.8^a	11.1 ± 1.0^a
SLA ($\text{mm}^2 \cdot \text{mg}^{-1}$)	8.577 ± 2.614^a	9.905 ± 7.252^a
Leaf area (mm^2)	2747.1 ± 3130.8^a	2470.4 ± 2839.4^a
Seed weight (mg)	640.1 ± 371.2^a	669.4 ± 426.1^a
Fruit length (mm)	43.8 ± 17.7^a	42.1 ± 29.4^a
Wood density ($\text{g} \cdot \text{cm}^{-3}$)	0.685 ± 0.017^a	0.674 ± 0.047^a
Vessel area (mm^2)	0.009 ± 0.001^a	0.010 ± 0.003^a
Leaf N content ($\text{mg} \cdot \text{g}^{-1}$)	28.08 ± 4.12^a	28.85 ± 5.12^a
Leaf P content ($\text{mg} \cdot \text{g}^{-1}$)	1.37 ± 0.18^a	1.47 ± 0.22^a

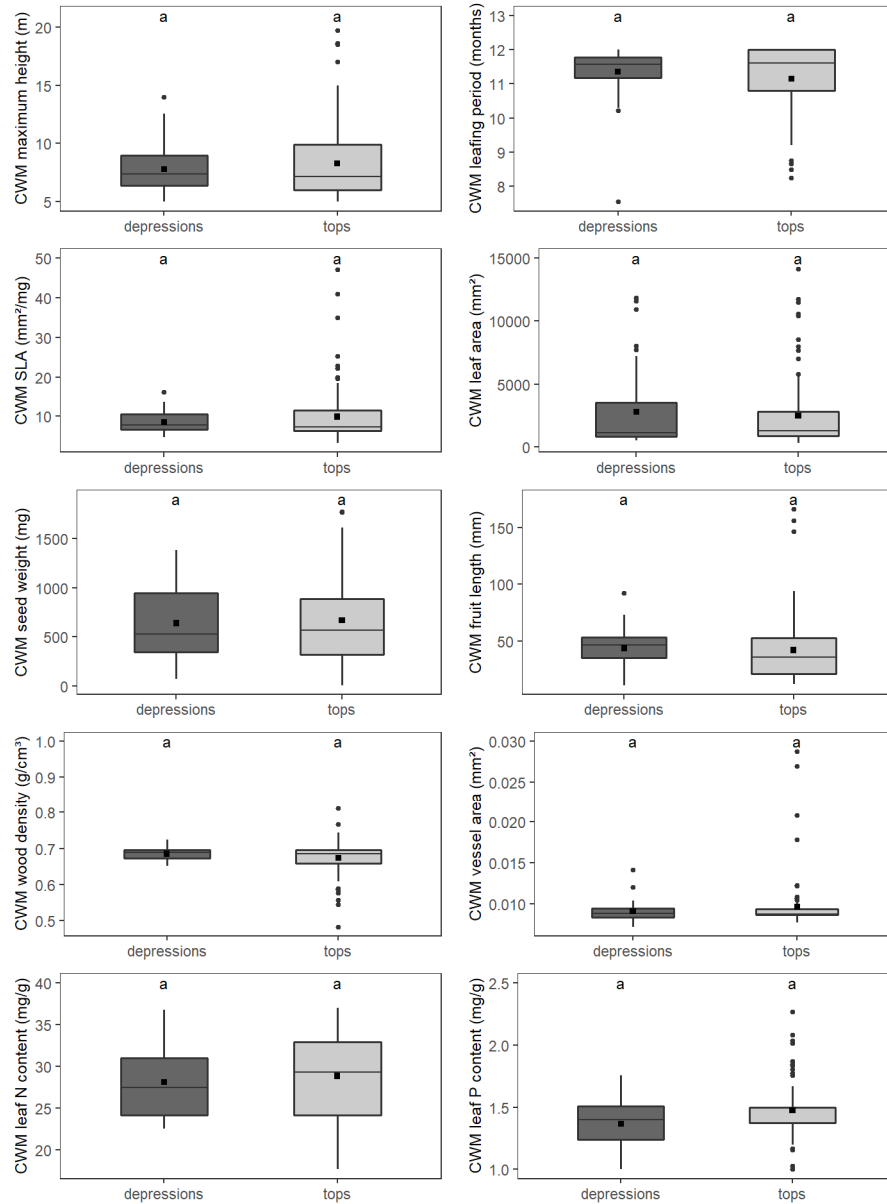


Figure A25.1 – CWM of ten continuous traits according to the topography (n plots = 139). The solid lines inside the boxes represent the medians and the squares represent the means. Letters indicate if the means are significantly different according to the Wilcoxon's tests ($P < 0.01$).

Table A25.3 – Response diversity (means $\pm$ standard deviations of FDis) to the three responses for each functional group per topographic element ($n = 139$ plots, 43 depressions, 96 tops). Different upper letters in a row indicate significant difference between tops and depressions ($P < 0.05$).

Function	Response	FG	Depressions	Tops
Primary productivity	Drought	FG-pp1	0.31 ± 0.34^b	0.10 ± 0.25^a
		FG-pp2	0.62 ± 0.47^b	0.42 ± 0.56^a
	Fire	FG-pp1	0.68 ± 0.57^b	0.29 ± 0.51^a
		FG-pp2	0.29 ± 0.25^b	0.23 ± 0.34^a
	Grazing	FG-pp1	0.52 ± 0.50^b	0.23 ± 0.44^a
		FG-pp2	0.39 ± 0.30^b	0.28 ± 0.39^a
Biogeochemical cycles	Drought	FG-bc1	0.13 ± 0.33^b	0.00^a
		FG-bc2	0.20 ± 0.48^b	0.00^a
		FG-bc3	0.67 ± 0.48^b	0.42 ± 0.45^a
	Fire	FG-bc1	0.13 ± 0.35^b	0.00^a
		FG-bc2	0.15 ± 0.33^b	0.00^a
		FG-bc3	0.74 ± 0.49^b	0.49 ± 0.51^a
	Grazing	FG-bc1	0.10 ± 0.30^b	0.00^a
		FG-bc2	0.07 ± 0.18^b	0.00^a
		FG-bc3	0.75 ± 0.48^b	0.52 ± 0.50^a

Appendices to Chapter 7

Appendix 26: Trees present since 1980 within the study area

Some of the individuals inventoried in 2015-2017 have been geotagged by direct localization on the field with a GPS point (for the inventory of 2017), or *a posteriori* on the Bing map images with the help of sketches drawn during the inventory of 2015.

Among these individuals, we were able to find some of them on the aerial images from 1980. This indicates that these trees have more than 35 years, age to which we must add the number of years necessary to be visible on aerial photos.

For the ones that were not found on aerial photos, it is not necessarily because they were not present in 1980. It can also be due to the low quality of some images, preventing us to distinguish individual tree with certainty, or because we did not have the images covering the plots.

Table A26.1 – Number of geotagged individuals, per species, visible on the aerial photos from 1980.

Species	Number of individuals
<i>Acacia tortilis</i>	3
<i>Adansonia digitata</i>	3
<i>Balanites aegyptiaca</i>	15
<i>Combretum glutinosum</i>	8
<i>Grewia bicolor</i>	1
<i>Guiera senegalensis</i>	1
<i>Sclerocarya birrea</i>	59
Total	91

Bibliography

- Abdourhamane, H., Rabiou, H., Diouf, A., Morou, B., Mahamane, A. and Bellefontaine, R. (2017) *Structure démographique et répartition spatiale des populations de Sclerocarya birrea (A.Rich.) Hochst. du secteur sabélien du Niger*. Bois et forêts des tropiques, 333 (3): 55-66.
- Aguirre-Gutiérrez, J., Malhi, Y., Lewis, S.L., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., Baker, T.R., Gvozdevaite, A., Hubau, W., Moore, S., Peprah, T., Ziemińska, K., Phillips, O.L. and Oliveras, I. (2020) *Long-term droughts may drive drier tropical forests towards increased functional, taxonomic and phylogenetic homogeneity*. Nature Communications, 11 (1): 3346.
- Akpo, A., Goudiaby, V.A., Grouzis, M. and Le Houérou, H.N. (2005) *Tree shade effects on soils and environmental factors in a savanna of Senegal*. West African Journal of Applied Ecology, 7: 41-52.
- Akpo, L.E. and Grouzis, M. (1996) *Influence du couvert sur la régénération de quelques espèces ligneuses sabéliennes (Nord Sénégal, Afrique occidentale)*. Webbia, 50 (2): 247-263.
- Ali, M., Saadou, M. and Jean, L. (2007) *Phénologie de quelques espèces ligneuses du parc national du « W » (Niger)*. Science et changements planétaires / Sécheresse, 18 (4): 354-358.
- Anchang, Y.J., Prihodko, L., Kaptué, T.A., Ross, W.C., Ji, W., Kumar, S.S., Lind, B., Sarr, A.M., Diouf, A.A. and Hanan, P.N. (2019) *Trends in Woody and Herbaceous Vegetation in the Savannas of West Africa*. Remote Sensing, 11 (5): 1-17.
- Anyamba, A. and Tucker, C.J. (2005) *Analysis of Sahelian vegetation dynamics using NOAA-AVHRR NDVI data from 1981–2003*. Journal of Arid Environments, 63 (3): 596-614.
- Arbonnier, M. (2009) *Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest (3^e édition)*. CIRAD, MHNM: Montpellier, France, 573 p.
- Arbonnier, M. (2019) *Arbres, arbustes et lianes d'Afrique de l'Ouest (4^e édition)*. Éditions Quae, 776 p.

- Argaw, M., Teketay, D. and Olsson, M. (1999) *Soil seed flora, germination and regeneration pattern of woody species in an Acacia woodland of the Rift Valley in Ethiopia*. Journal of Arid Environments, 43 (4): 411-435.
- Assouma, H. (2016) *Approche écosystémique du bilan des gaz à effet de serre d'un territoire sylvo-pastoral sabélien: contribution de l'élevage*. Thèse de doctorat, AgroParisTech. 230 p.
- Aubin, I., Munson, A.D., Cardou, F., Burton, P.J., Isabel, N., Pedlar, J.H., Paquette, A., Taylor, A.R., Delagrangé, S., Kebli, H., Messier, C., Shipley, B., Valladares, F., Kattge, J., Boisvert-Marsh, L. and McKenney, D. (2016) *Traits to stay, traits to move: a review of functional traits to assess sensitivity and adaptive capacity of temperate and boreal trees to climate change*. Environmental Reviews, 24 (2): 164-186.
- Aubréville, A. (1949) *Climats, forêts et désertification de l'Afrique tropicale*. Société d'éditions géographiques, maritimes et coloniales. Paris, 351 p.
- Ayantunde, A.A., Hiernaux, P., Briejer, M., Udo, H. and Tabo, R. (2009) *Uses of local plant species by agropastoralists in South-western Niger*. Ethnobotany Research & Applications, 7: 53-66.
- Bakhoun, A. (2013) *Dynamique des ressources fourragères: indicateurs de résilience des parcours communautaires de Tessekere au Ferlo (Nord- Senegal)*. Thèse de doctorat, Université Cheikh Anta Diop de Dakar. 120 p.
- Barbier, N., Couteron, P., Lejoly, J., Deblauwe, V. and Lejeune, O. (2006) *Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems*. Journal of Ecology, 94 (3): 537-547.
- Bargués Tobella, A., Reese, H., Almaw, A., Bayala, J., Malmer, A., Laudon, H. and Ilstedt, U. (2014) *The effect of trees on preferential flow and soil infiltrability in an agroforestry parkland in semiarid Burkina Faso*. Water Resources Research, 50 (4): 3342-3354.
- Barral, H. (1982) *Le Ferlo des forages : gestion ancienne et actuelle de l'espace pastoral : étude de géographie humaine*. ORSTOM: Dakar, 85 p.
- Barral, H., Bénéfice, E., Boudet, G., Denis, J.P., Wispelaere, G.d., Diaite, I., Diaw, O.T., Dieye, K., Doutre, M.P., Meyer, J.F., Noël, J., Parent, G., Piot, J., Planchenault, D., Santoir, C., Valentin, C., Valenza, J. and Vassiliades, G. (1983) *Systèmes de production d'élevage au Sénégal dans la région du Ferlo : synthèse de fin d'études d'une équipe de recherches pluridisciplinaire*. ORSTOM: Paris, 172 p.
- Bastin, J.-F., Berrahmouni, N., Grainger, A., Maniatis, D., Mollicone, D., Moore, R., Patriarca, C., Picard, N., Sparrow, B., Abraham, E.M., Aloui, K., Atesoglu, A., Attore, F., Bassüllü, Ç., Bey, A., Garzuglia, M., García-Montero, L.G., Groot, N., Guerin, G., Laestadius, L., Lowe, A.J.,

- Mamane, B., Marchi, G., Patterson, P., Rezende, M., Ricci, S., Salcedo, I., Díaz, A.S.-P., Stolle, F., Surappaeva, V. and Castro, R. (2017) *The extent of forest in dryland biomes*. Science, 356 (6338): 635.
- Baumer, M. (1983) *Notes on trees and shrubs in arid and semi-arid regions*. Food and Agriculture Organization of the United Nations: Rome, 270 p.
- Bellefontaine, R. (1997) Synthèse des espèces des domaines sahélien et soudanien qui se multiplient naturellement par voie végétative. In *Fonctionnement et gestion des écosystèmes contractés sahéliens*. J.M. d'Herbès, J.-M.K. Ambouta and R. Régis Peltier (eds.), John Libbey Eurotext, Paris, pp. 95-104.
- Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. and Nyström, M. (2003) *Reserves, Resilience and Dynamic Landscapes*. AMBIO: A Journal of the Human Environment, 32 (6): 389-396.
- Berdugo, M., Delgado-Baquerizo, M., Soliveres, S., Hernández-Clemente, R., Zhao, Y., Gaitán, J.J., Gross, N., Saiz, H., Maire, V., Lehmann, A., Rillig, M.C., Solé, R.V. and Maestre, F.T. (2020) *Global ecosystem thresholds driven by aridity*. Science, 367 (6479): 787.
- Bille, J.C. (1973) *Recherches écologiques sur une savane sahélienne du Sénégal septentrional : description de l'écosystème, biomasse végétale et production primaire*. Annales de l'Université d'Abidjan.Série E : Ecologie, 6 (2): 131-137.
- Bille, J.C. (1974) *Recherches écologiques sur une savane sahélienne du Ferlo septentrional, Sénégal: 1972, année sèche au Sabel*. La Terre et la Vie : Revue d'Ecologie Appliquée, 28 (1): 5-20.
- Bille, J.C. (1977) *Etude de la production primaire nette d'un écosystème sahélien*. Travaux et Documents de l'ORSTOM (65), ORSTOM, 86 p.
- Bille, J.C., Lepage, M. and Poupon, H. (1972) *Présentation de la zone d'étude de Fété-Olé (Sénégal)*. ORSTOM: Dakar, Sénégal, 54 p.
- Boudet, G. (1984) *Manuel sur les pâturages tropicaux et les cultures fourragères*. 4ème edn. Ministère des relations extérieures: Paris, France, 267 p.
- Brand, F. and Jax, K. (2007) *Focusing the meaning(s) of resilience: resilience as a descriptive concept and a boundary object*. Ecology and society : a journal of integrative science for resilience and sustainability, 12: 23.
- Brandt, M., Hiernaux, P., Rasmussen, K., Tucker, C.J., Wigneron, J.-P., Diouf, A.A., Herrmann, S.M., Zhang, W., Kergoat, L., Mbow, C., Abel, C., Auda, Y. and Fensholt, R. (2019) *Changes in rainfall distribution promote woody foliage production in the Sabel*. Communications Biology, 2: 133.

- Brandt, M., Hiernaux, P., Tagesson, T., Verger, A., Rasmussen, K., Diouf, A.A., Mbow, C., Mougin, E. and Fensholt, R. (2016) *Woody plant cover estimation in drylands from Earth Observation based seasonal metrics*. Remote Sensing of Environment, 172: 28-38.
- Brandt, M., Mbow, C., Diouf, A.A., Verger, A., Samimi, C. and Fensholt, R. (2015) *Ground- and satellite-based evidence of the biophysical mechanisms behind the greening Sahel*. Global Change Biology, 21 (4): 1610-1620.
- Brandt, M., Rasmussen, K., Hiernaux, P., Herrmann, S., Tucker, C.J., Tong, X., Tian, F., Mertz, O., Kergoat, L., Mbow, C., David, J.L., Melocik, K.A., Dendoncker, M., Vincke, C. and Fensholt, R. (2018) *Reduction of tree cover in West African woodlands and promotion in semi-arid farmlands*. Nature Geoscience, 11 (5): 328-333.
- Brandt, M., Romankiewicz, C., Spiekermann, R. and Samimi, C. (2014) *Environmental change in time series – An interdisciplinary study in the Sahel of Mali and Senegal*. Journal of Arid Environments, 105: 52-63.
- Brandt, M., Tappan, G., Diouf, A.A., Beye, G., Mbow, C. and Fensholt, R. (2017) *Woody vegetation die off and regeneration in response to rainfall variability in the West African Sahel*. Remote Sensing, 9 (39): 1-21.
- Braun-Blanquet, J. (1932) *Plant sociology: The study of plant communities*. 1st ed. McGraw-Hill Book Company, inc.: New York and London.
- Breman, H. and De Ridder, N. (1991) *Manuel sur les pâturages des pays sahéliens*. ACCT-CTA-Karthala: Wageningen, Pays-Bas, 488 p.
- Breman, H. and Kessler, J.J. (1995) *Woody plants in agro-ecosystems of semi-arid regions*. Springer-Verlag: Berlin, 340 p.
- Breman, H. and Sissoko, F. (1998) *L'intensification agricole au Sahel*. Broché, 996 p.
- Briske, D.D., Fuhlendorf, S.D. and Smeins, F.E. (2003) *Vegetation dynamics on rangelands: a critique of the current paradigms*. Journal of Applied Ecology, 40 (4): 601-614.
- Burke, A. (2006) *Savanna trees in Namibia—Factors controlling their distribution at the arid end of the spectrum*. Flora - Morphology, Distribution, Functional Ecology of Plants, 201 (3): 189-201.
- Carpenter, S., Walker, B., Anderies, J.M. and Abel, N. (2001) *From metaphor to measurement: resilience of what to what ?* Ecosystems, 4: 765-781.
- Cervigni, R. and Morris, M. (2015) *Affronter la sécheresse dans les zones arides de l'Afrique : Des possibilités de renforcer la résilience*. Collection L'Afrique en développement. Banque mondiale, Washington, DC, 277 p.

- Cesaro, J.D., Magrin, G. and Ninot, O. (2010) *Atlas de l'élevage au Sénégal. Commerce et territoires*. Publication du projet de recherche ATP Icare: Dakar, Sénégal, 32 p.
- Charles-Dominique, T., Davies, T.J., Hempson, G.P., Bezeng, B.S., Daru, B.H., Kabongo, R.M., Maurin, O., Muasya, A.M., van der Bank, M. and Bond, W.J. (2016) *Spiny plants, mammal browsers, and the origin of African savannas*. *Proceedings of the National Academy of Sciences*, 113 (38): E5572.
- Charreau, C. and Fauck, R. (1965) *Les sols du Sénégal*. Etudes sénégalaises n°9. ORSTOM, Saint-Louis, Sénégal, 45 p.
- Chillo, V., Anand, M. and Ojeda, R. (2011) *Assessing the Use of Functional Diversity as a Measure of Ecological Resilience in Arid Rangelands*. *Ecosystems*, 14 (7): 1168-1177.
- Chiveu, C.J., Dangasuk, O.G., Omunyin, M.E. and Wachira, F.N. (2009) *Quantitative variation among Kenyan populations of Acacia senegal (L.) Willd. for gum production, seed and growth traits*. *New Forests*, 38 (1): 1.
- Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., López, R. and Medlyn, B.E. (2018) *Triggers of tree mortality under drought*. *Nature*, 558 (7711): 531-539.
- CILSS. (2016) *Landscapes of West Africa - a window on a changing world*. U.S. Geological Survey EROS: 47914 252nd St, Garretson, SD 57030, UNITED STATES, 236 p.
- Clanet, J.-C. and Gillet, H. (1980) *Le Commiphora africana, véritable arbre fourrager sahélien*. In *Les fourrages ligneux en Afrique: état des connaissances actuelles*. H.N. Le Houerou (ed.), Centre International Pour l'Elevage en Afrique, pp. 431-433.
- Colombo, R.C., Favetta, V., Yamamoto, L.Y., Alves, G.A.C., Abati, J., Takahashi, L.S.A. and Faria, R.T.d. (2015) *Biometric description of fruits and seeds, germination and imbibition pattern of desert rose [Adenium obesum (Forssk.), Roem. & Schult.]*. *Journal of Seed Science*, 37: 206-213.
- Condit, R., Sukumar, R., Hubbell, S.P. and Foster, R.B. (1998) *Predicting population trends from size distributions: a direct test in a tropical tree community*. *The American Naturalist*, 152 (4): 495-509.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., az, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.t., Morgan, H.D., Heijden, M.G.A.v.d., Pausas, J.G. and Poorter, H. (2003) *A handbook of protocols for standardised and easy measurement of plant functional traits worldwide*. *Australian Journal of Botany*, 51 (4): 335-380.

- Cornet, A. (1976) *Observations préliminaires sur les propriétés physiques et le bilan hydrique des sols dans les écosystèmes sabéliens étudiés*. ORSTOM: Dakar, Sénégal, 16 p.
- Cornet, A. (1978) *Observations sur les précipitations dans la partie centrale du secteur sabélien sénégalais*. Notes Africaines (158): 34-42.
- Cornet, A. (1981) *Le bilan hydrique et son rôle dans la production de la strate herbacée de quelques phytocénoses sabéliennes au Sénégal*. Phd. Université des Sciences et Techniques du Languedoc. 353 p.
- Cornet, A. (1992) Relations entre la structure spatiale des peuplements végétaux et le bilan hydrique des sols de quelques phytocénoses en zone aride. In *L'aridité : une contrainte au développement : caractérisation, réponses biologiques, stratégies des sociétés*. E. Le Floch, M. Grouzis, A. Cornet et al. (eds.), ORSTOM, Paris, pp. 245-265.
- Coughenour, M.B. and Detling, J.K. (1986) *Acacia tortilis seed germination responses to water potential and nutrients*. African Journal of Ecology, 24 (3): 203-205.
- Craven, D., Filotas, E., Angers, V.A. and Messier, C. (2016) *Evaluating resilience of tree communities in fragmented landscapes: linking functional response diversity with landscape connectivity*. Diversity and Distributions, 22 (5): 505-518.
- Curtis, J.T. (1959) *The vegetation of Wisconsin: an ordination of plant communities*. The University of Wisconsin Press: Madison, Wisconsin, USA, 663 p.
- Daget, P. and Gaston, A. (1999) *Flotrop: constitution d'une base de données sur les pâturages d'Afrique tropicale septentrionale*. Sécheresse, 10 (3): 183-189.
- Danthu, P., Ickowicz, A., Friot, D., Manga, D. and Sarr, A. (1996) *Effet du passage par le tractus digestif des ruminants domestiques sur la germination des graines de légumineuses ligneuses des zones tropicales sèches*. Revue Elev. Méd. vét. Pays trop., 49 (3): 235-241.
- Dardel, C., Kergoat, L., Hiernaux, P., Mougin, E., Grippa, M. and Tucker, C.J. (2014) *Re-greening Sahel: 30 years of remote sensing data and field observations (Mali, Niger)*. Remote Sensing of Environment, 140: 350-364.
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Martins da Silva, P., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A. and Harrison, P.A. (2010) *Towards an assessment of multiple ecosystem processes and services via functional traits*. Biodiversity and Conservation, 19 (10): 2873-2893.
- De Bie, S., Ketner, P., Paasse, M. and Geerling, C. (1998) *Woody plant phenology in the West Africa savanna*. Journal of Biogeography, 25 (5): 883-900.

- de Wispelaere, G. (1980) *Les photographies aériennes témoins de la dégradation du couvert ligneux dans un géosystème sabélien sénégalais - Influence de la proximité d'un forage*. Cahiers ORSTOM.Série Sciences humaines, 27 (3-4): 155-166.
- Dembélé, F., Picard, N., Karembé, M. and Birnbaum, P. (2006) *Tree vegetation patterns along a gradient of human disturbance in the Sahelian area of Mali*. Journal of Arid Environments, 64 (2): 284-297.
- Dendoncker, M. (2013) *Structure, dynamique et utilisations de la ressource ligneuse dans le Ferlo (Sénégal)*. Mémoire de master. Université catholique de Louvain. 112 p.
- Dendoncker, M. and Vincke, C. (2020) *Low topographic positions enhance woody vegetation stability in the Ferlo (Senegalese Sabel)*. Journal of Arid Environments, 175: 104087.
- Diallo, M.D., Goalbaye, T., Mahamat-Saleh, M., Sarr, P.S., Masse, D., Wood, S.A., Diop, A., Dick, R.P., Diop, A. and Guisse, A. (2017) *Effects of major woody species of the Senegalese Great Green Wall on N mineralization and microbial biomass in soils*. Bois et forêts des tropiques, 333 (3): 43-54.
- Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Díez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. and Zak, M.R. (2004) *The plant traits that drive ecosystems: Evidence from three continents*. Journal of Vegetation Science, 15 (3): 295-304.
- Diémé, J.S., Diouf, M., Armas, C., Rusch, G.M. and Pugnaire, F.I. (2017) *Functional groups of Sahelian trees in a semiarid agroforestry system of Senegal*. Journal of Plant Ecology, 11 (3): 375-384.
- Diop, A.T., Sy, O., Ickowicz, A. and Touré, I. (2003) *Politique d'hydraulique et gestion de l'espace et des ressources dans la région sylvopastorale du Sénégal, Ferlo*. In *Actes du colloque international Umr Sagert*, Montpellier, France, 9 p.
- Diouf, J.C. (2011) *Dynamique du peuplement ligneux au Ferlo (Nord-Sénégal), conséquences et perspectives pour une gestion durable*. Thèse de doctorat, Université Cheikh Anta Diop de Dakar. 262 p.
- Diouf, J.C., Akpo, L.E., Ickowicz, A., Lesueur, D. and Chotte, J.-L. (2005) *Dynamique des peuplements ligneux et pratiques pastorales au Sahel*

- (Ferlo, Sénégal). In *Conférence Internationale : Biodiversité Science et Gouvernance*. R. Barbault and J.P. Le Duc (eds.), MNHN, Paris, pp. 9.
- Dounias, E. (2000) *Revue de la littérature ethnobotanique pour l'Afrique centrale et l'Afrique de l'Ouest*. Bulletin du Réseau Africain d'Ethnobotanique, 2: 5-117.
- Dukku, U.H. (2010) *Plants for bees: Guiera senegalensis, an important nectar plant in the savanna*. Bee World, 87 (4): 77.
- Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. and Norberg, J. (2003) *Response diversity, ecosystem change, and resilience*. Frontiers in Ecology and the Environment, 1 (9): 488-494.
- Epule, E., Peng, C., Lepage, L. and Chen, Z. (2014) *The causes, effects and challenges of Sabelian droughts: a critical review*. Reg Environ Change, 14: 145-156.
- Eriksson, O. (1996) *Regional Dynamics of Plants: A Review of Evidence for Remnant, Source-Sink and Metapopulations*. Oikos, 77 (2): 248-258.
- Fall, S.T. (1991) *Digestibilité in vitro et dégradabilité in situ dans le rumen de ligneux fourragers disponibles sur pâturages naturels au Sénégal: premiers résultats*. Revue d'élevage et de médecine vétérinaire des pays tropicaux, 44 (3): 345-354.
- FAO (2010) *Lignes directrices pour la gestion durable des forêts en zones arides d'Afrique subsaharienne*. Document de travail sur les les Forêts et la Foresterie en zones arides No. 1, 56 p.
- FAO (2019) *Trees, forests and land use in drylands: the first global assessment. Full report.*, FAO forestry paper, Rome, 193 p.
- Farahat, A.E., Galal, M.T., El-Midany, M.M. and Hassan, M.L. (2016) *Phenology, biomass and reproductive characteristics of Calotropis procera (Aiton) W.T. Aiton in South Cairo, Egypt*. Rendiconti Lincei, 27 (2): 197-204.
- Fensholt, R., Rasmussen, K., Kaspersen, P., Huber, S., Horion, S. and Swinnen, E. (2013) *Assessing Land Degradation/Recovery in the African Sabel from Long-Term Earth Observation Based Primary Productivity and Precipitation Relationships*. Remote Sensing, 5 (2).
- Fick, S.E. and Hijmans, R.J. (2017) *WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas*. International Journal of Climatology, 37 (12): 4302-4315.
- Flynn, D.F.B., Mirotchnick, N., Jain, M., Palmer, M.I. and Naeem, S. (2011) *Functional and phylogenetic diversity as predictors of biodiversity: ecosystem-function relationships*. Ecology, 92 (8): 1573-1581.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. and Holling, C.S. (2004) *Regime Shifts, Resilience, and Biodiversity in Ecosystem*

- Management*. Annual Review of Ecology, Evolution, and Systematics, 35 (1): 557-581.
- Fotius, G., Naegele, A. and Valenza, J. (1967) *Lexique des noms vernaculaires concernant la flore du Nord et de l'Est du Sénégal*. ORSTOM: Dakar, 75 p. multigr. p.
- Frich, P., Alexander, L.V., Della-Marta, P., Gleason, B., Haylock, M., Klein Tank, A.M.G. and Peterson, T. (2002) *Observed coherent changes in climatic extremes during the second half of the twentieth century*. Climate Research, 19: 193-212.
- Gallopin, G.C. (2006) *Linkages between vulnerability, resilience and adaptive capacity*. Global Environmental Change, 16: 293-303.
- Garner, R.D. and Witkowski, E.T.F. (1997) *Variations in seed size and shape in relation to depth of burial in the soil and pre-dispersal predation in Acacia nilotica, Acacia tortilis and Dichrostachys cinerea*. South African Journal of Botany, 63 (6): 371-377.
- Garnier, E. and Navas, M.-L. (2012) *A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review*. Agron. Sustain. Dev., 32 (2): 365-399.
- Gebrekirostos, A., Mitlöhner, R., Teketay, D. and Worbes, M. (2008) *Climate–growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia*. Trees, 22 (5): 631-641.
- Gebrekirostos, A., Teketay, D., Fetene, M. and 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 (1–3): 259-267.
- Gonzalez, P. (2001) *Desertification and a shift of forest species in the West African Sahel*. Climate Research, 17 (2): 217-228.
- Gonzalez, P., Tucker, C.J. and Sy, H. (2012) *Tree density and species decline in the African Sahel attributable to climate*. Journal of Arid Environments, 78: 55-64.
- Gower, J.C. (1971) *A General Coefficient of Similarity and Some of Its Properties*. Biometrics, 27 (4): 857-871.
- Grime, J.P. (1977) *Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory*. The American Naturalist, 111 (1982): 1169-1194.
- Grime, J.P. (1998) *Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects*. Journal of Ecology, 86 (6): 902-910.

- Grimm, V. and Wissel, C. (1997) *Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion*. *Oecologia*, 109 (3): 323-334.
- Gross, N., Bagousse-Pinguet, Y.L., Liancourt, P., Berdugo, M., Gotelli, N.J. and Maestre, F.T. (2017) *Functional trait diversity maximizes ecosystem multifunctionality*. *Nature Ecology & Evolution*, 1 (5): 0132.
- Grouzis, M. and Akpo, A. (1996) *Dynamique des interactions arbre-herbe en milieu sabélien: influence de l'arbre sur la structure et le fonctionnement de la strate herbacée*. In *Actes sur la réunion thématique sur l'acacia au Sénégal* Dakar, Sénégal. ORSTOM-ISRA, pp. 37-46.
- Grouzis, M. and Akpo, L.E. (2006) *Interactions arbre-herbe au Sabel*. *Science et changements planétaires/Sécheresse*, 17 (1-2): 318-325.
- Grouzis, M. and Le Floch, E. (2003) *Un arbre au désert : Acacia raddiana*. IRD: Paris, 313 p.
- Guissé, N., Ouattara, B. and LeBloas, J. (1987) *Répertoire des travaux de cartographie, levés terrestres et couvertures aériennes du bassin du fleuve Sénégal*. OMVS, USAID, SGN Senegal, Dakar, 15 p.
- Guissou, T.G. (2001) *La symbiose mycorhizienne à arbuscules chez des espèces d'arbres: diversité des glomales, dépendance mycorhizienne, utilisation des phosphates naturels et tolérance à un stress hydrique*. Phd. Université de Ouagadougou (Burkina Faso). 227 p.
- Haines-Young, R. and Potschin, M. (2018) Common International Classification of Ecosystem Services (CICES) V5.1 and Guidance on the Application of the Revised Structure. Available from www.cices.eup.
- Hanan, N.P., Prevost, Y., Diouf, A. and Diallo, O. (1991) *Assessment of desertification around deep wells in the Sabel using satellite imagery*. *Journal of Applied Ecology*, 28 (1): 173-186.
- Hänke, H., Börjeson, L., Hylander, K. and Enfors-Kautsky, E. (2016) *Drought tolerant species dominate as rainfall and tree cover returns in the West African Sabel*. *Land Use Policy*, 59: 111-120.
- Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M., Geamăna, N., Geertsema, W., Lommelen, E., Meiresonne, L. and Turkelboom, F. (2014) *Linkages between biodiversity attributes and ecosystem services: A systematic review*. *Ecosystem Services*, 9: 191-203.
- Hein, L. and De Ridder, N. (2006) *Desertification in the Sabel: a reinterpretation*. *Global Change Biology*, 12 (5): 751-758.

- Hejmanová, P., Hejman, M., Camara, A.A. and Antonínová, M. (2010) *Exclusion of livestock grazing and wood collection in dryland savannah: an effect on long-term vegetation succession*. African Journal of Ecology, 48 (2): 408-417.
- Helm, C.V., Scott, S.L. and Witkowski, E.T.F. (2011) *Reproductive potential and seed fate of Sclerocarya birrea subsp. caffra (marula) in the low altitude savannas of South Africa*. South African Journal of Botany, 77 (3): 650-664.
- Herrmann, S.M., Anyamba, A. and Tucker, C.J. (2005) *Recent trends in vegetation dynamics in the African Sahel and their relationship to climate*. Global Environmental Change-human and Policy Dimensions, 15 (4): 394-404.
- Herrmann, S.M., Diouf, A.A. and Sall, I. (2020) *Beyond bioproductivity: Engaging local perspectives in land degradation monitoring and assessment*. Journal of Arid Environments, 173: 104002.
- Herrmann, S.M. and Hutchinson, C.F. (2005) *The changing contexts of the desertification debate*. Journal of Arid Environments, 63 (3): 538-555.
- Herrmann, S.M., Sall, I. and Sy, O. (2014) *People and pixels in the Sahel: a study linking coarse-resolution remote sensing observations to land users' perceptions of their changing environment in Senegal*. Ecology and Society, 19 (3): 29.
- Herrmann, S.M. and Tappan, G.G. (2013) *Vegetation impoverishment despite greening: a case study from central Senegal*. Journal of Arid Environments, 90: 55-66.
- Hiernaux, P. (2006) *Le suivi écologique de Widou Thiengoly : un patrimoine scientifique à développer et valoriser. Rapport de mission, PAPF. Saint-Louis, Sénégal*, 47 p.
- Hiernaux, P., Cissé, M.I., Diarra, L. and de Leeuw, P.N. (1994) *Fluctuations saisonnières de la feuillaison des arbres et des buissons sahéliens. Conséquences pour la quantification des ressources fourragères*. Revue d'élevage et de médecine vétérinaire des pays tropicaux, 47 (1): 117-125.
- Hiernaux, P., Diarra, L., Trichon, V., Mougin, E., Soumaguel, N. and Baup, F. (2009) *Woody plant population dynamics in response to climate changes from 1984 to 2006 in Sahel (Gourma, Mali)*. Journal of Hydrology, 375 (1-2): 103-113.
- Hiernaux, P. and Le Houérou, H.N. (2006) *Les parcours du Sahel*. Sécheresse, 17 (1-2): 51-71.
- Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. and Thompson, K. (1999) *Allocating C-S-R Plant Functional Types: A Soft Approach to a Hard Problem*. Oikos, 85 (2): 282-294.
- Holling, C.S. (1973) *Resilience and Stability of Ecological Systems*. Annual Review of Ecology and Systematics, 4 (1): 1-23.

- Holling, C.S. (1996) Engineering resilience versus ecological resilience. In *Engineering within ecological constraints*, National Academy Press, Washigton, D.C., USA, pp. 31-44.
- Holm, S. (1979) *A Simple Sequentially Rejective Multiple Test Procedure*. Scandinavian Journal of Statistics, 6 (2): 65-70.
- Ickowicz, A., Ancey, V., Corniaux, C., Duteurtre, G., Pocard-Chappuis, R., Touré, I., Vall, E. and Wane, A. (2012) *Crop–livestock production systems in the Sabel – increasing resilience for adaptation to climate change and preserving food security*. In *Building Resilience for Adaptation to Climate Change in the Agriculture Sector, a joint FAO/OECD Workshop* Rome, Italy, pp. 261-294.
- IPBES (2018) *The IPBES regional assessment report on biodiversity and ecosystem services for Africa*. E. Archer, L. Dziba, K.J. Mulongoy *et al.*, Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany, 492 p.
- IPCC (2014a) *Climate Change 2014: impacts, adaptation, and vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* V.R. Barros, C.B. Field, D.J. Dokken *et al.*, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 688 p.
- IPCC (2014b) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I,II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Core Writing Team, R.K. Pachauri and L.A. Meyer. IPCC, Geneva, Switzerland, 151 p.
- Jahel, C., Lenormand, M., Seck, I., Apolloni, A., Toure, I., Faye, C., Sall, B., Lo, M., Diaw, C.S., Lancelot, R. and Coste, C. (2020) *Mapping livestock movements in Sabelian Africa*. Scientific Reports, 10 (1): 8339.
- Joker, D. (2000a) *Acacia senegal (L.) Willd.* Seed Leaflet (5), University of Copenhagen, 2 p.
- Joker, D. (2000b) *Acacia seyal Del.* Seed Leaflet (34), University of Copenhagen, 2 p.
- Joker, D. (2000c) *Acacia tortilis (Forssk.) Hayne*. Seed Leaflet (19), University of Copenhagen, 2 p.
- Joker, D. (2000d) *Faidherbia albida (Del.) A. Chev.* Seed Leaflet (28), University of Copenhagen, 2 p.
- Joker, D. (2003) *Ziziphus mauritiana*. Seed Leaflet (85), University of Copenhagen, 2 p.

- Joker, D. and Erdey, D. (2003) *Sclerocarya birrea* (A. Rich.) Hochst. Seed Leaflet (72), University of Copenhagen, 2 p.
- Jones, A., Breuning-Madsen, H., Brossard, M., Dampha, A., Deckers, J., Dewitte, O., Gallali, T., Hallett, S., Jones, R., Kilasara, M., Le Roux, P., Michéli, E., Montanarella, L., Spaargaren, O., Thiombiano, L., Van Ranst, E., Yemefack, M. and Zougmore, R., (eds.). (2013) *Soil atlas of Africa*. European Commission, Publications Office of the European Union: Luxembourg, 173 p.
- Karlson, M. and Ostwald, M. (2016) *Remote sensing of vegetation in the Sudano-Sabelian zone: A literature review from 1975 to 2014*. Journal of Arid Environments, 124: 257-269.
- Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., BÖNisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin Iii, F.S., Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-MÉNdez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., KÜHN, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., LlusiÀ, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., MÜLLer, S.C., Nadrowski, K., Naeem, S., Niinemets, Ü., NÖLLert, S., NÜSke, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., OrdoÑez, J., Overbeck, G., Ozinga, W.A., PatiÑO, S., Paula, S., Pausas, J.G., PeÑUelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. and Wirth, C. (2011) TRY – a global database of plant traits. Global Change Biology, 17 (9): 2905-2935.
- Kgope, B.S. and Musil, C.F. (2004) *Differential photosynthetic responses of broad- and fine-leaved savanna trees to elevated temperatures*. South African Journal of Botany, 70 (5): 760-766.

- Khouma, M. (2002) *Les grands types de sols du Sénégal*. <http://www.fao.org/docrep/005/Y3948F/y3948f07.htm> (5 novembre 2012).
- Kindt, R., Ordonez, J., Smith, E., Orwa, C., D., H., Kehlenbeck, K., E., L., Munjuga, M., Mwanzia, L., Sinclair, F. and Jamnadass, R. (2013) ICRAF Species Switchboard, Version 1.0. World Agroforestry Centre.
- Kirchmair, I., Schmidt, M., Zizka, G., Erpenbach, A. and Hahn, K. (2012) *Biodiversity Islands in the savanna: analysis of the phytodiversity on termite mounds in Northern Benin*. Flora and Vegetatio Sudano-Sambesica, 15: 3-14.
- Kizito, F., Dragila, M., Sène, M., Lufafa, A., Diedhiou, I., Dick, R.P., Selker, J.S., Dossa, E., Khouma, M., Badiane, A. and Ndiaye, S. (2006) *Seasonal soil water variation and root patterns between two semi-arid shrubs co-existing with Pearl millet in Senegal, West Africa*. Journal of Arid Environments, 67 (3): 436-455.
- Kusserow, H. (2017) *Desertification, resilience, and re-greening in the African Sahel – a matter of the observation period?* Earth Syst. Dynam., 8 (4): 1141-1170.
- Kuznetsova, A., Brockhoff, P.B. and Christensen, R.H.B. (2017) *lmerTest Package: Tests in Linear Mixed Effects Models*. Journal of Statistical Software, 82 (13).
- Ky-Dembele, C., Tigabu, M., Bayala, J., Ouédraogo, S.J. and Odén, P.C. (2007) *The relative importance of different regeneration mechanisms in a selectively cut savanna-woodland in Burkina Faso, West Africa*. Forest Ecology and Management, 243 (1): 28-38.
- L'Hote, Y., Mahé, G.I.L., Somé, B. and Triboulet, J.P. (2002) *Analysis of a Sahelian annual rainfall index from 1896 to 2000; the drought continues*. Hydrological Sciences Journal, 47 (4): 563-572.
- Lahoreau, G., Barot, S., Gignoux, J., Hoffmann, W.A., Setterfield, S.A. and Williams, P.R. (2006) *Positive effect of seed size on seedling survival in fire-prone savannas of Australia, Brazil and West Africa*. Journal of Tropical Ecology, 22 (6): 719-722.
- Laliberté, E. and Legendre, P. (2010) *A distance-based framework for measuring functional diversity from multiple traits*. Ecology, 91 (1): 299-305.
- Laliberté, E., Legendre, P. and Shipley, B. (2014) *FD: measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12.
- Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C., Aubin, I., Bonser, S.P., Ding, Y., Fraterrigo, J.M., McNamara, S., Morgan, J.W., Merlos, D.S., Vesk, P.A. and Mayfield, M.M. (2010) *Land-use intensification reduces functional redundancy and response diversity in plant communities*. Ecology Letters, 13 (1): 76-86.

- Lavorel, S. and Garnier, E. (2002) *Predicting Changes in Community Composition and Ecosystem Functioning from Plant Traits: Revisiting the Holy Grail*. *Functional Ecology*, 16 (5): 545-556.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G. and Douzet, R. (2011) *Using plant functional traits to understand the landscape distribution of multiple ecosystem services*. *Journal of Ecology*, 99 (1): 135-147.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quétier, F., Thébault, A. and Bonis, A. (2008) *Assessing functional diversity in the field – methodology matters!* *Functional Ecology*, 22 (1): 134-147.
- Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M. and Maestre, F.T. (2019) *Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality*. *Proceedings of the National Academy of Sciences*, 116 (17): 8419.
- Le Houérou, H.N. (1980a) Composition chimique et valeur nutritive des fourrages ligneux en Afrique tropicale occidentale. In *Les fourrages ligneux en Afrique: état actuel des connaissances*. H.N. Le Houérou (ed.), Centre International Pour l'Elevage en Afrique, pp. 259-284.
- Le Houérou, H.N. (1980b) Le rôle des ligneux fourragers dans les zones sahélienne et soudanienne. In *Le rôle des ligneux fourragers dans les zones sahélienne et soudanienne*. H.N. Le Houérou (ed.), Centre International Pour l'Elevage en Afrique, pp. 85-94.
- Le Houérou, H.N. (1980c) *Les fourrages ligneux en Afrique: état actuel des connaissances*. Centre International Pour l'Elevage en Afrique: Addis Abeba, Ethiopie, 481 p.
- Le Houérou, H.N. (1980d) *The rangelands of the Sahel*. *Journal of Range Management*, 33 (1): 41-46.
- Le Houérou, H.N. (1989) *The grazing land ecosystems of the African Sahel*. Springer-Verlag Berlin Heidelberg: Berlin, Germany, 282 p.
- Lebel, T. and Ali, A. (2009) *Recent trends in the Central and Western Sahel rainfall regime (1990–2007)*. *Journal of Hydrology*, 375 (1): 52-64.
- Legendre, P. and Legendre, L. (2012) Chapter 9 - Ordination in reduced space. In *Developments in Environmental Modelling*. P. Legendre and L. Legendre (eds.), Elsevier, pp. 425-520.
- Legras, G., Loiseau, N., Gaertner, J.-C., Poggiale, J.-C. and Gaertner-Mazouni, N. (2019) *Assessing functional diversity: the influence of the number of the functional traits*. *Theoretical Ecology*.

- Lindenmayer, D.B. and Laurance, W.F. (2017) *The ecology, distribution, conservation and management of large old trees*. Biological Reviews, 92 (3): 1434-1458.
- Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J. and Valladares, F. (2012) *Extreme climatic events and vegetation: the role of stabilizing processes*. Global Change Biology, 18 (3): 797-805.
- Lykke, A.M. (1998) *Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information*. Biodiversity and Conservation, 7 (10): 1261-1275.
- Lykke, A.M., Fog, B. and Madsen, J.E. (1999) *Woody vegetation changes in the Sahel of Burkina Faso assessed by means of local knowledge, aerial photos, and botanical investigations*. Danish Journal of Geography, 2: 57-68.
- Lykke, A.M., Kristensen, M.K. and Ganaba, S. (2004) *Valuation of local use and dynamics of 56 woody species in the Sahel*. Biodiversity and Conservation, 13: 1961-1990.
- Manoli, C., Ancey, V., Corniaux, C., Ickowicz, A., Dedieu, B. and Moulin, C.H. (2014) *How do pastoral families combine livestock herds with other livelihood security means to survive? The case of the Ferlo area in Senegal*. Pastoralism, 4 (1): 3.
- Maranz, S. (2009) *Tree mortality in the African Sahel indicates an anthropogenic ecosystem displaced by climate change*. Journal of Biogeography, 36 (6): 1181-1193.
- Mason, N.W.H., Mouillot, D., Lee, W.G. and Wilson, J.B. (2005) *Functional richness, functional evenness and functional divergence: the primary components of functional diversity*. Oikos, 111 (1): 112-118.
- May, J.F., Guengant, J.-P. and Brooke, T.R. (2015) *Demographic challenges of the Sahel* <http://www.prb.org/Publications/Articles/2015/sahel-demographics.aspx> (28.10, 2016).
- Mayus, M., Van Keulen, H. and Stroosnijder, L. (1998) *A model of tree-crop competition for windbreak systems in the Sahel: description and evaluation*. Agroforestry Systems, 43 (1): 183-201.
- Mbow, C., Brandt, M., Ouedraogo, I., de Leeuw, J. and Marshall, M. (2015) *What four decades of earth observation tell us about land degradation in the Sahel?* Remote Sensing, 7: 4048-4067.
- McKee, T.B., Doesken, N.J. and Kleist, J. (1993) *The relationship of drought frequency and duration to time scales*. Anaheim, California. American Meteorological Society, Boston, MA, pp. 179-184.
- MEA. (2005) *Ecosystems and human well-being: Synthesis*. Island Press: Washington, DC, 137 p.

- Mensah, S., Veldtman, R., Assogbadjo, A.E., Glèlè Kakaï, R. and Seifert, T. (2016) *Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance*. Ecology and Evolution, 6 (20): 7546-7557.
- Midgley, J., Sawe, T., Abanyam, P., Hintsa, K. and Gacheru, P. (2016) *Spinescent East African savannah acacias also have thick bark, suggesting they evolved under both an intense fire and herbivory regime*. African Journal of Ecology, 54: 118-120.
- Midgley, J.J. (1998) *Dispersibility, cost and allometry of tumblers (Combretum, Combretaceae) and parachutes (Leucadendron, Proteaceae) of different size*. Plant Systematics and Evolution, 211 (3/4): 141-147.
- Miehe, S. (1994) *Inventaire et suivi de la végétation dans le périmètre expérimental à Widou Thiengohy dans le cadre du Projet Sénégal-Allemand "Exploitation sylvopastorale des Sols dans le Nord du Sénégal/Modèle d'aménagement sylvo-pastoral des terres en vue de la lutte contre la désertification"*. 112 p.
- Miehe, S. (2002) *Inventaire et suivi de la végétation dans le périmètre expérimental de Widou Thiengohy dans le cadre du projet Sénégal-allemand d'autopromotion pastorale dans le Ferlo (PAPF), Rapport final*. Saint-Louis, Sénégal, 57 p.
- Miehe, S., Kluge, J., von Wehrden, H. and Retzer, V. (2010) *Long-term degradation of Sahelian rangeland detected by 27 years of field study in Senegal*. Journal of Applied Ecology, 47 (3): 692-700.
- Miller, F., Osbahr, H., Boyd, E., Thomalla, F., Bharwani, S., Ziervogel, G., Walker, B., Birkmann, J., van der Leeuw, S., Rockstrom, J., Hinkel, J., Downing, T., Folke, C. and Nelson, D. (2010) *Resilience and vulnerability: complementary of conflicting concepts ?* Ecology and Society, 15 (3).
- Miller, M.F. and Coe, M. (1993) *Is it advantageous for Acacia seeds to be eaten by ungulates ?* Oikos, 66 (2): 364-368.
- Milton, S.J., Dean, W.R.J., Plessis, M.A.d. and Siegfried, W.R. (1994) *A Conceptual Model of Arid Rangeland Degradation*. BioScience, 44 (2): 70-76.
- Mirzabaev, A., Wu, J., Evans, J., Garcia-Oliva, F., Hussein, I.A.G., Iqbal, M.H., Kimutai, J., Knowles, T., Meza, F., DNedjraoui, D., Tena, F., Turkes, M., Vazquez, R.J. and Welts, M. (2019) Desertification. In *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. J.S. P.R. Shukla, E. Calvo Buendia, V. Masson-Delmotte, H.-O. Pörtner, P.Z. D.C. Roberts, R. Slade, S. Connors, R. van Diemen, M. Ferrat, E. Haughey, S. Luz, S. Neogi, M. Pathak, J. Petzold, and P.V. J. Portugal Pereira, E. Huntley, K. Kissick, M. Belkacemi, J. Malley (eds.), pp. 249-343.

- Mitchell, T. (2018) Sahel Precipitation Index (20-10N, 20W-10E), 1901-2017. doi:10.6069/H5MW2F2Q
- Mori, A.S., Furukawa, T. and Sasaki, T. (2013) *Response diversity determines the resilience of ecosystems to environmental change*. Biological Reviews, 88 (2): 349-364.
- Mouchet, M.A., Villéger, S., Mason, N.W.H. and Mouillot, D. (2010) *Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules*. Functional Ecology, 24 (4): 867-876.
- Mougin, E., Hiernaux, P., Kergoat, L., Grippa, M., de Rosnay, P., Timouk, F., Le Dantec, V., Demarez, V., Lavenu, F., Arjounin, M., Lebel, T., Soumaguel, N., Ceschia, E., Mougnot, B., Baup, F., Frappart, F., Frison, P.L., Gardelle, J., Gruhier, C., Jarlan, L., Mangiarotti, S., Sanou, B., Tracol, Y., Guichard, F., Trichon, V., Diarra, L., Soumaré, A., Koité, M., Dembélé, F., Lloyd, C., Hanan, N.P., Damesin, C., Delon, C., Serça, D., Galy-Lacaux, C., Seghier, J., Becerra, S., Dia, H., Gangneron, F. and Mazzega, P. (2009) *The AMMA-CATCH Gourma observatory site in Mali: Relating climatic variations to changes in vegetation, surface hydrology, fluxes and natural resources*. Journal of Hydrology, 375 (1–2): 14-33.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. and Bellwood, D.R. (2013) *A functional approach reveals community responses to disturbances*. Trends in Ecology & Evolution, 28 (3): 167-177.
- Mouillot, D., Villéger, S., Scherer-Lorenzen, M. and Mason, N.W.H. (2011) *Functional Structure of Biological Communities Predicts Ecosystem Multifunctionality*. PLOS ONE, 6 (3): e17476.
- Naeem, S. (1998) *Species Redundancy and Ecosystem Reliability*. Conservation Biology, 12 (1): 39-45.
- Ndiaye, O., Diallo, A., Wood, S.A. and Guisse, A. (2014) *Structural Diversity of Woody Species in the Senegalese Semi-Arid Zone - Ferlo*. American Journal of Plant Sciences, 5 (3): 416-426.
- Ngom, D. (2008) *Définition d'indicateurs de gestion durable des ressources sylvo-pastorales au Ferlo (Nord-Sénégal)*. Thèse de doctorat, Université Cheikh Anta Diop de Dakar. 148 p.
- Nicholson, S. (2005) *On the question of the "recovery" of the rains in the West African Sahel*. Journal of Arid Environments, 63: 615-641.
- Nicholson, S.E. (1995) Sahel, West Africa. In *Encyclopedia of Environmental Biology*. Vol.3, Academic Press, pp. 261-275.
- Nicholson, S.E. (2001) *Climatic and environmental change in Africa during the last two centuries*. Climate Research, 17 (2): 123-144.

- Nicholson, S.E. (2013) *The West African Sabel: A Review of Recent Studies on the Rainfall Regime and Its Interannual Variability*. ISRN Meteorology, 2013: 32 p.
- Nicholson, S.E., Some, B. and Kone, B. (2000) *An Analysis of Recent Rainfall Conditions in West Africa, Including the Rainy Seasons of the 1997 El Niño and the 1998 La Niña Years*. Journal of Climate, 13 (14): 2628-2640.
- Nicholson, S.E., Tucker, C.J. and Ba, M.B. (1998) *Desertification, drought, and surface vegetation: an example from the West African Sabel*. Bulletin of the American Meteorological Society, 79: 815-829.
- Nielsen, T.T., Rasmussen, K., Mbow, C. and Touré, A. (2003) *The fire regime of Senegal and its determinants*. Geografisk Tidsskrift-Danish Journal of Geography, 103 (1): 43-53.
- Nock, C.A., Vogt, R.J. and Beisner, B.E. (2016) Functional Traits. In *eLS*, John Wiley & Sons, Ltd.
- O'Brien, M.J., Engelbrecht, B.M.J., Joswig, J., Pereyra, G., Schuldt, B., Jansen, S., Kattge, J., Landhäusser, S.M., Levick, S.R., Preisler, Y., Väänänen, P. and Macinnis-Ng, C. (2017) *A synthesis of tree functional traits related to drought-induced mortality in forests across climatic zones*. Journal of Applied Ecology, 54 (6): 1669-1686.
- Ochoa-Hueso, R., Eldridge, D.J., Delgado-Baquerizo, M., Soliveres, S., Bowker, M.A., Gross, N., Le Bagousse-Pinguet, Y., Quero, J.L., García-Gómez, M., Valencia, E., Arredondo, T., Beinticenco, L., Bran, D., Cea, A., Coaguila, D., Dougill, A.J., Espinosa, C.I., Gaitán, J., Guuroh, R.T., Guzman, E., Gutiérrez, J.R., Hernández, R.M., Huber-Sannwald, E., Jeffries, T., Linstädter, A., Mau, R.L., Monerris, J., Prina, A., Pucheta, E., Stavi, I., Thomas, A.D., Zaady, E., Singh, B.K. and Maestre, F.T. (2018) *Soil fungal abundance and plant functional traits drive fertile island formation in global drylands*. Journal of Ecology, 106 (1): 242-253.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. and Wagner, H. (2019) *vegan: Community Ecology Package*. R package version 2.5-5. <https://CRAN.R-project.org/package=vegan>.
- Olsson, L., Eklundh, L. and Ardö, J. (2005) *A recent greening of the Sabel-trends, patterns and potential causes*. Journal of Arid Environments, 63 (3): 556-566.
- Osborne, C.P., Charles-Dominique, T., Stevens, N., Bond, W.J., Midgley, G. and Lehmann, C.E.R. (2018) *Human impacts in African savannas are mediated by plant functional traits*. New Phytologist, 220: 10-24.

- Penning de Vries, F.W.T. and Djiteye, M.A. (1982) *La productivité des pâturages sabeliens : une étude des sols, des végétations et de l'exploitation de cette ressource naturelle*. Pudoc: Wageningen, 525 p.
- Pennington, R.T., Lehmann, C.E.R. and Rowland, L.M. (2018) *Tropical savannas and dry forests*. *Current Biology*, 28 (9): R541-R545.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S. and Cornelissen, J.H.C. (2013) *New handbook for standardised measurement of plant functional traits worldwide*. *Australian Journal of Botany*, 61 (3): 167-234.
- Petchey, O.L. and Gaston, K.J. (2006) *Functional diversity: back to basics and looking forward*. *Ecology Letters*, 9 (6): 741-758.
- Poorter, L. and Markesteijn, L. (2008) *Seedling Traits Determine Drought Tolerance of Tropical Tree Species*. *Biotropica*, 40 (3): 321-331.
- Poupon, H. (1979) *Etude de la phénologie de la strate ligneuse à Fété-Olé (Sénégal septentrional) de 1971 à 1977*. *Bulletin de l'IFAN.Série A : Sciences Naturelles* (t. 41.- 1): 44-91.
- Poupon, H. (1980) *Structure et dynamique de la strate ligneuse d'une steppe sabélienne au nord du Sénégal*. OS : Ouvrages scientifiques, ORSTOM. 351 p.
- Poupon, H. and Bille, J.C. (1974) *Recherches écologiques sur une savane sabélienne du Ferlo septentrional, Sénégal: influence de la sécheresse de l'année 1972-1973 sur la strate ligneuse*. *La Terre et la Vie : Revue d'Ecologie Appliquée*, 1: 49-75.
- Prince, S.D., De Colstoun, E.B. and Kravitz, L.L. (1998) *Evidence from rain-use efficiencies does not indicate extensive Sabelian desertification*. *Global Change Biology*, 4 (4): 359-374.
- R core team (2018) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org/>.
- Rasmussen, K., Brandt, M., Tong, X., Hiernaux, P., Diouf, A.A., Assouma, M.H., Tucker, C.J. and Fensholt, R. (2018) *Does grazing cause land degradation? Evidence from the sandy Ferlo in Northern Senegal*. *Land Degradation & Development*, 29: 4337–4347.
- Rasmussen, K., D'haen, S., Fensholt, R., Fog, B., Horion, S., Nielsen, J.O., Rasmussen, L.V. and Reenberg, A. (2016) *Environmental change in the Sabel:*

- reconciling contrasting evidence and interpretations*. Reg Environ Change, 16 (3): 673-680.
- Reynolds, J.F., Maestre, F.T., Kemp, P.R., Stafford-Smith, D.M. and Lambin, E. (2007) Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences. In *Terrestrial Ecosystems in a Changing World*. J.G. Canadell, D.E. Pataki and L.F. Pitelka (eds.), Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 247-257.
- Ribeiro, L.C., Barbosa, E.R.M., Langevelde, F. and Borghetti, F. (2015) *The importance of seed mass for the tolerance to heat shocks of savanna and forest tree species*. Journal of Vegetation Science, 26 (6): 1102-1111.
- Robert, N. and Björn, E. (2000) *Stem basic density and bark proportion of 45 woody species in young savanna coppice forests in Burkina Faso*. Ann. For. Sci., 57 (2): 143-153.
- Royal Botanic Gardens Kew. (1999) Survey of Economic Plants for Arid and Semi-Arid Lands (SEPASAL) database. <http://apps.kew.org/sepasalweb/sepaweb>
- Royal Botanic Gardens Kew. (2008) Seed Information Database (SID) Version 7.1. Royal Botanic Gardens Kews. <http://data.kew.org/sid/>
- Sacande, M., Ronne, C., Sanon, M. and Joker, D. (2006) *Adansonia digitata* L. Seed Leaflet (109), University of Copenhagen, 2 p.
- Sacande, M. and Sanogo, S. (2007) *Anogeissus leiocarpus* (DC.) Guill. & Perr. Seed Leaflet (119), University of Copenhagen, 2 p.
- Sacande, M., Sanon, M. and Schmidt, L.H. (2007a) *Sterculia setigera* Delile. Seed Leaflet (134), University of Copenhagen, 2 p.
- Sacande, M., Vautier, H., Sanon, M. and Schmidt, L.H. (2007b) *Dalbergia melanoxydon* Guill. & Perr. Seed Leaflet (135), University of Copenhagen, 2 p.
- Salack, S., Muller, B. and Gaye, A.T. (2011) *Rain-based factors of high agricultural impacts over Senegal. Part I: integration of local to sub-regional trends and variability*. Theoretical and Applied Climatology, 106 (1): 1-22.
- Sankaran, M. (2019) *Droughts and the ecological future of tropical savanna vegetation*. Journal of Ecology, 107 (4): 1531-1549.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., 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. and Zambatis, N. (2005) *Determinants of woody cover in African savannas*. *Nature*, 438 (7069): 846-849.
- Sanon, M., Sacandé, M. and Schmidt, L.H. (2007) *Combretum aculeatum Vent.* Seed Leaflet (127), University of Copenhagen, 2 p.
- Santiago, L.S., Bonal, D., De Guzman, M.E. and Ávila-Lovera, E. (2016) Drought Survival Strategies of Tropical Trees. In *Tropical Tree Physiology: Adaptations and Responses in a Changing Environment*. G. Goldstein and L.S. Santiago (eds.), Springer International Publishing, Cham, pp. 243-258.
- Schlesinger, W.H. and Pilmanis, A.M. (1998) *Plant-soil Interactions in Deserts*. *Biogeochemistry*, 42 (1): 169-187.
- Schmidt, L.H. and Joker, D. (2000) *Balanites aegyptiaca (L.) Del.* Seed Leaflet (21), University of Copenhagen, 2 p.
- Schmidt, L.H. and Mbora, A. (2008a) *Acacia nilotica (L.) Del.* Seed Leaflet (137), University of Copenhagen, 2 p.
- Schmidt, L.H. and Mbora, A. (2008b) *Commiphora africana (A. Rich.) Engel.* Seed Leaflet (138), University of Copenhagen, 2 p.
- Schmidt, M., Traoré, S., Ouédraogo, A., Mbayngone, E., Ouédraogo, O., Zizka, A., Kirchmair, I., Kaboré, E., Tindano, E., Thiombiano, A., Hahn, K. and Zizka, G. (2013) *Geographical Patterns of Woody Plants' Functional Traits in Burkina Faso*. *Candollea*, 68 (2): 197-207.
- Scholes, R.J. and Archer, S.R. (1997) *Tree-Grass Interactions in Savannas*. *Annual Review of Ecology and Systematics*, 28 (1): 517-544.
- Seghier, J., Do, F., Devineau, J.-L. and Fournier, A. (2012) Phenology of woody species along the climatic gradient in West Tropical Africa. In *Phenology and climate change*. X. Zhang (ed.), InTech, pp. 320.
- Sellers, P.J. (1985) *Canopy reflectance, photosynthesis and transpiration*. *International Journal of Remote Sensing*, 6 (8): 1335-1372.
- Sen, D.N. (1968) *Ecology of desert plants and observations on their seedlings. II. Germination behaviour of seeds in Asclepiadaceae*. *Österreichische botanische Zeitschrift*, 115 (1): 18-27.
- Seye, N.K.L. and Cissé, K. (2019) Chapitre IX: Elevage. In *Situation économique et sociale du Sénégal en 2016*, Agence Nationale de la Statistique et de la Démographie, pp. 215-222.
- Sinare, H. and Gordon, L.J. (2015) *Ecosystem services from woody vegetation on agricultural lands in Sudano-Sahelian West Africa*. *Agriculture, Ecosystems & Environment*, 200: 186-199.

- Sinclair, A.R.E. and Fryxell, J.M. (1985) *The Sabel of Africa: ecology of a disaster*. Canadian Journal of Zoology, 63 (5): 987-994.
- Sivakumar, M.V.K., Maidoukia, A. and Stern, R.D. (1993) Agroclimatology of West Africa: Niger. In *ICRISAT Information Bulletin*, Patancherup.
- Siyum, Z.G. (2020) *Tropical dry forest dynamics in the context of climate change: syntheses of drivers, gaps, and management perspectives*. Ecological Processes, 9 (1): 25.
- Smith, M.D. (2011) *An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research*. Journal of Ecology, 99 (3): 656-663.
- Sop, T.K., Oldeland, J., Bognounou, F., Schmiedel, U. and Thiombiano, A. (2012) *Ethnobotanical knowledge and valuation of woody plants species: a comparative analysis of three ethnic groups from the sub-Sabel of Burkina Faso*. Environment, Development and Sustainability, 14 (5): 627-649.
- Sop, T.K., Oldeland, J., Schmiedel, U., Ouedraogo, I. and Thiombiano, A. (2011) *Population structure of three woody species in four ethnic domains of the sub-sabel of Burkina Faso*. Land Degradation & Development, 22 (6): 519-529.
- Spiekermann, R., Brandt, M. and Samimi, C. (2015) *Woody vegetation and land cover changes in the Sabel of Mali (1967–2011)*. International Journal of Applied Earth Observation and Geoinformation, 34: 113-121.
- Stancioff, A., Staljanssens, M. and Tappan, G. (1986) *Cartographie et télédétection des ressources de la République du Sénégal: étude de la géologie, de l'hydrogéologie, des sols, de la végétation et des potentiels d'utilisation des sols*. Institut de télédétection, South Dakota State University: USA, 653 p.
- Steentoft, M. (1988) *Flowering plants in West Africa*. Cambridge University Press: New York, 350 p.
- Sterk, M., Gort, G., Klimkowska, A., van Ruijven, J., van Teeffelen, A.J.A. and Wamelink, G.W.W. (2013) *Assess ecosystem resilience: Linking response and effect traits to environmental variability*. Ecological Indicators, 30 (0): 21-27.
- Suliman, H.M., Buchroithner, M.F. and Elhag, M.M. (2012) *Use of local knowledge for assessing vegetation changes in the Southern Gadarif Region, Sudan*. African Journal of Ecology, 50 (2): 233-242.
- Tappan, G. (1986) *Végétation et utilisation des terres*. In *Cartographie et télédétection des ressources de la République du Sénégal: étude de la géologie, de l'hydrogéologie, des sols, de la végétation et des potentiels d'utilisation des sols*, Institut de télédétection, South Dakota State University, USA, pp. 482-629.
- Tappan, G.G., Sall, M., Wood, E.C. and Cushing, M. (2004) *Ecoregions and land cover trends in Senegal*. Journal of Arid Environments, 59 (3): 427-462.

- Tatem, A.J. (2017) *WorldPop, open data for spatial demography*. Scientific Data, 4: 170004.
- Taugourdeau, S. (2014) *Effets of management and climate on the plant functional diversity related to ecosystem services of permanent grasslands in Europe*. Université de Lorraine. 193 p.
- Taugourdeau, S., Daget, P., Chatelain, C., Mathieu, D., Juanes, X., Huguenin, J. and Ickowicz, A. (2019) *FLOTROP, a massive contribution to plant diversity data for open ecosystems in northern tropical Africa*. Scientific Data, 6: 118.
- Taugourdeau, S., Villerd, J., Plantureux, S., Huguenin-Elie, O. and Amiaud, B. (2014) *Filling the gap in functional trait databases: use of ecological hypotheses to replace missing data*. Ecology and Evolution, 4 (7): 944-958.
- Tezara, W., Colombo, R., Coronel, I. and Marin, O. (2011) *Water relations and photosynthetic capacity of two species of Calotropis in a tropical semi-arid ecosystem*. Annals of Botany, 107: 397-405.
- Thébaud, B. (1990) *Politiques d'hydraulique pastorale et gestion de l'espace au Sahel*. Cahiers des Sciences Humaines, 26 (1-2): 13-31.
- Thébaud, B. and Batterbury, S. (2001) *Sahel pastoralists: opportunism, struggle, conflict and negotiation. A case study from eastern Niger*. Global Environmental Change, 11: 69-78.
- Tilman, D. (2001) Functional diversity. In *Encyclopedia of biodiversity*. S.A. Levin (ed.), Academic Press, pp. 109-120.
- Touré, I., Diop, A.T., Akpo, E., Dieye, S., Bakhoun, A. and Wade, A. (2011) *Tache ECOS: vulnérabilité de l'agro-écosystème aux changements climat et occupation des sols. Caractérisation de l'espace et des ressources des sites du Ferlo (site de Téssékéré)*. ANR-ECLIS (PPZS, CIRAD, CSE, ISRA, UCAD, ENNA), 25 p.
- Touré, I., Ickowicz, A., Wane, A., Garba, I. and Gerber, P. (2012) *Atlas des évolutions des systèmes pastoraux au Sahel*. FAO et CIRAD, 32 p.
- Touré, O. (1990) *Where herders don't herd anymore: experience from the Ferlo, northern Senegal*. IIED, International Institute for Environment and Development, 22 p.
- Tréca, B. and Tamba, S. (1997) *Rôle des oiseaux sur la régénération du ligneux Boscia senegalensis (pers.) Lam. en savane sahélienne au Nord Sénégal*. Revue d'Ecologie : la Terre et la Vie, 52: 239-260.
- Tucker, C.J. (1979) *Red and photographic infrared linear combinations for monitoring vegetation*. Remote Sensing of Environment, 8 (2): 127-150.

- Tybirk, K. (1991) *Regeneration of woody legumes in Sabel*. Botanical Institute Aarhus University: Denmark, 81 p.
- UN. (1992) *Agenda 21: The United Nations plan of action from Rio*. United Nations, New York.
- Valencia, E., Maestre, F.T., Le Bagousse-Pinguet, Y., Quero, J.L., Tamme, R., Börger, L., García-Gómez, M. and Gross, N. (2015) *Functional diversity enhances the resistance of ecosystem multifunctionality to aridity in Mediterranean drylands*. New Phytologist, 206 (2): 660-671.
- Valenza, J. and Diallo, A.K. (1972a) Etude des pâturages naturels du Nord du Sénégal, 1 carte couleur à 1/200 000 en 3 coupons. In *Etudes agrostologie*, Maisons Alfort : IEMVT, Dakar, Senegal, 331 p.
- Valenza, J. and Diallo, A.K. (1972b) *Etude des pâturages naturels du Nord Sénégal*. Etude agrostologique. GERDAT-IEMVT, Maisons-Alfort, France, 311 p.
- Van den Bilcke, N., De Smedt, S., Simbo, D.J. and Samson, R. (2013) *Sap flow and water use in African baobab (Adansonia digitata L.) seedlings in response to drought stress*. South African Journal of Botany, 88: 438-446.
- Vassal, J. (1998) Les acacias au Sénégal - Taxonomie, écologie, principaux intérêts. In *L'Acacia au Sénégal: 3-5 décembre 1996, Dakar, Sénégal*, IRD Editions, pp. 15-33.
- Vautier, H., Sanon, M., Sacandé, M. and Schmidt, L.H. (2007) *Combretum glutinosum* Perrot. ex DC. Seed Leaflet (128), University of Copenhagen, 2 p.
- Villéger, S., Mason, N.W.H. and Mouillot, D. (2008) *New multidimensional functional diversity indices for a multifaceted framework in functional ecology*. Ecology, 89 (8): 2290-2301.
- Vincke, C., Diédhiou, I. and Grouzis, M. (2010) *Long term dynamics and structure of woody vegetation in the Ferlo (Senegal)*. Journal of Arid Environments, 74 (2): 268-276.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. (2007) *Let the concept of trait be functional!* Oikos, 116 (5): 882-892.
- Wageningen University. (2020) Prota4u - Plant Resources of Tropical Africa Database. . <https://www.prota4u.org/>
- Walker, B., Kinzig, A. and Langridge, J. (1999) *Plant Attribute Diversity, Resilience, and Ecosystem Function: The Nature and Significance of Dominant and Minor Species*. Ecosystems, 2 (2): 95-113.

- Weiher, E., Werf, A.v.d., Thompson, K., Roderick, M., Garnier, E. and Eriksson, O. (1999) *Challenging Theophrastus: A Common Core List of Plant Traits for Functional Ecology*. Journal of Vegetation Science, 10 (5): 609-620.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. and Wright, I.J. (2002) *Plant ecological strategies: some leading dimensions of variation between species*. Annual Review of Ecology and Systematics, 33: 125-159.
- Westoby, M., Walker, B. and Noy-Meir, I. (1989) *Opportunistic management for rangelands not at equilibrium*. Journal of Range Management, 42 (4): 266-274.
- Wezel, A. and Lykke, A.M. (2006) *Woody vegetation change in Sahelian West Africa: evidence from local knowledge*. Environment, Development and Sustainability, 8 (4): 553-567.
- Wheeler, E. (2011) *Insidewood - a web resource for hardwood anatomy*. IAWA Journal, 32 (2): 199-211.
- White, F. (1983) *The vegetation of Africa*. UNESCO: Paris, 356 p.
- White, R.P. and Nackoney, J. (2003) *Drylands, people, and ecosystem goods and services: a web-based geospatial analysis*. Washington, DC 58 p.
- Whitford, W. and Wade, E. (2002) *Ecology of desert systems*. Academic Press, an Elsevier Science Imprint: San Diego, California, 343 p.
- Wickens, G.E. (1980) Autres utilisations des espèces ligneuses. In *Le rôle des ligneux fourragers dans les zones sahélienne et soudanienne*. H.N. Le Houerou (ed.), Centre International Pour l'Elevage en Afrique, pp. 153-180.
- Wiegand, K., Ward, D., Thulke, H.H. and Jeltsch, F. (2000) *From snapshot information to long-term population dynamics of Acacias by a simulation model*. Plant Ecology, 150 (1-2): 97-114.
- Wilson, T.B. and Witkowski, E.T.F. (1998) *Water requirements for germination and early seedling establishment in four African savanna woody plant species*. Journal of Arid Environments, 38 (4): 541-550.
- Witkowski, E.T.F. and Garner, R.D. (2000) *Spatial distribution of soil seed banks of three African savanna woody species at two contrasting sites*. Plant Ecology, 149 (1): 91-106.
- Yachi, S. and Loreau, M. (1999) *Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis*. Proc Natl Acad Sci U S A, 96 (4): 1463-1468.
- Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C. and Chave, J. (2009a)

Global Wood Density Database. Data from: Towards a worldwide wood economics spectrum. Dryad. doi: 10.5061/dryad.234

Zanne, A.E., Westoby, M., Falster, D.S., Ackerly, D.D., Loarie, S.R., Arnold, S.E.J. and Coomes, D. (2009b) Global Vessel Database. Data from: Angiosperm wood structure: global patterns in vessel anatomy and their relationship to wood density and potential conductivity. Dryad. doi: 10.5061/dryad.1138

Zuur, A., Ieno, E.N., Wlaker, N., Saveliev, A.A. and Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag New York, 574 p.

Zwarts, L., Bijlsma, R.G. and van der Kamp, J. (2018) *Large decline of birds in Sahelian rangelands due to loss of woody cover and soil seed bank*. Journal of Arid Environments, 155: 1-15.

Curriculum vitae

Publications

Dendoncker, M. and Vincke, C. (2020) Low topographic positions enhance woody vegetation stability in the Ferlo (Senegalese Sahel). *Journal of Arid Environments*, 175: 104087.

Brandt, M., Rasmussen, K., Hiernaux, P., Herrmann, S., Tucker, C.J., Tong, X., Tian, F., Mertz, O., Kergoat, L., Mbow, C., David, J.L., Melocik, K.A., **Dendoncker, M.**, Vincke, C. and Fensholt, R. (2018) Reduction of tree cover in West African woodlands and promotion in semi-arid farmlands. *Nature Geoscience*, 11 (5): 328-333.

Dendoncker, M., Ngom, D. and Vincke, C. (2015) Trees dynamics (1955-2012) and their uses in the Senegal's Ferlo region: insights from a historical vegetation database, local knowledge and field inventories. *Bois et forêts des tropiques*, 326 (4): 25-41.

In review or in press

Brandt, M., Tucker, C.J., Kariryaa, A., Rasmussen, K., Abel, C., Small, J., Chave, J., Rasmussen, L. V., Hiernaux, P., Diouf, A.A., Kergoat, L., Mertz, O., Igel, C., Gieseke, F., Schöning, J., Li, S., Melocik, K., Meyer, J., Sinno, S., Romero, E., Glennie, E., Montagu, A., **Dendoncker, M.**, Fensholt, R.. *An unexpectedly large count of trees in the West African Sahara and Sabel*. *Nature*, in press.

Dendoncker, M., Brandt, M., Rasmussen, K., Taugourdeau, S., Fensholt, R., Tucker, C.J. and Vincke, C. *Woody vegetation changes from 1965 to 2018 in the Ferlo (Senegal) using high-resolution imagery and field surveys*, submitted at Regional Environmental Change and accepted with minor revision at the date of July 12 2020.

Bossoukpe Dagnon, M.F., Faye, E., Ndiaye, O., Diatta, S., Diatta, O., Diouf, A.A., **Dendoncker, M.**, Assouma, M. H., Taugourdeau, S. *Low-cost drones help measuring tree characteristics in Sahelian savannah*. Submitted at Journal of Arid Environments and accepted with major revision at the date of June 1 2020.

Conference presentations

Oral presentations

Dendoncker, M., Taugourdeau, S., Vincke, C. Evaluation préliminaire des contributions des ligneux à des services écosystémiques en zone sahélienne (exemple du Ferlo Sénégal). *In* Pastoralisme dans le courant des changements globaux: Défis, enjeux, perspectives. Dakar, Sénégal, 20-24 November 2017.

Dendoncker, M., Vincke, C. A preliminary study on woody vegetation dynamics (1955--2012) and its impacts on related provisioning services in the northern Ferlo. Green Arid: What do we know about the potential impacts of Greening Scenarios in semi--arid regions? Dakar, Senegal 15-17 April 2015.

Poster presentations

Dendoncker, M., Vincke, C. Woody resources temporal dynamics (1955-2015) and radial growth in the Ferlo (Senegal) as a mean to assess ecosystem stability. *In* Wood Science underpinning tropical forest ecology and management. Tervuren, Belgium, 26-29 May 2015.

Taugourdeau, S., Diouf, A.A., Mbaye, T., **Dendoncker, M.**, Ndiaye, O., Hiernaux, P., Juanes, X., Ickowicz, A. Facteurs écologiques impactant les communautés végétales ligneuses et herbacées des parcours du Ferlo entre 1970 et 1981. *In* Pastoralisme dans le courant des changements globaux: Défis, enjeux, perspectives. Dakar, Sénégal, 20-24 November 2017.