The Role of Shrub Agroforestry Systems in Increasing Food Security for the West African Sahel

DISSENYATION

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By

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Abstract

The West African Sahel (WAS) faces environmental and socioeconomic constraints that routinely threaten regional food security. Subsistence farmers must contend with drought, low soil fertility, and land degradation while sustaining livelihoods from rainfed agriculture without the aid of synthetic fertilizers and pesticides. Rapid population growth and climate change only exacerbate the challenges. Consequently, the WAS urgently needs scientifically-validated, sustainable agricultural systems to guarantee landscape conservation, to provide sufficient nutrient and water supplies, and to optimize crop productivity. A truly effective system for combating food insecurity, however, requires the adoption of local, low-cost inputs that simultaneously increase yields and coexist within the framework of the socio-economic and environmental demands of the region. This dissertation, therefore, examined the use of a ubiquitous and increasing component of the natural savanna ecosystem in the WAS – shrubs – to enhance the growth and yields of the staple crops, pearl millet (*Pennisetum glaucum*) and groundnut (*Arachis hypogaeae*).

The first research chapter (Chapter 2) investigated the long-term (eleven years) effect of a dominant, semi-evergreen shrub, *Piliostigma reticulatum*, on yields, soil fertility, soil carbon, and nutrient cycling at an experimental site in southern Senegal. The density of *P. reticulatum* was increased to 1000 shrubs ha$^{-1}$ in a split-plot factorial design with the presence or absence of shrubs as the main plot and different rates of
fertilizer as the subplot. Millet and groundnut were planted in a yearly rotation. The results showed a strong positive effect of *P. reticulatum* on millet water use efficiency, yields, and soil nutrients. The results also clearly demonstrated that this cropping system promotes C sequestration. Furthermore, the study showed, surprisingly, that the shrubs use water from the previous year’s rainy season for the following year’s growth which helps explain why *P. reticulatum* does not compete with crops for limited water.

Chapter 3 studied the long-term (twelve years) effect of another dominant shrub, *Guiera senegalensis*, to increase the soil quality, growth, and yields of millet and groundnut using the same experimental design as found in Chapter 2 (1500 shrubs ha\(^{-1}\)) but at a site in central Senegal with extremely sandy, degraded soils. The results unequivocally demonstrated that *G. senegalensis* could maintain yields and improve soil quality through limited rainfall. The mechanisms behind the shrub effect were examined more closely in this chapter: its effect on soil water content, temperature, and root growth between plants. There was a temporal offset between growth of *G. senegalensis* and millet roots. *G. senegalensis* primarily grew during the dry season, whereas millet grew during the rainy season which again shows why shrubs and crops do not compete for limited nutrients.

Chapter 4 reports the first-ever ecological survey of the beneficial symbiotic fungi, arbuscular mycorrhizae (AM), conducted in the rooting zone of *G. senegalensis* at four farmers’ fields in the Sahelian and Sudanian ecological zones of Senegal. These fungi simultaneously grow in the soil and infect roots, and the beneficial symbiosis is an exchange of nutrients for photosynthetically-fixed carbon from the plant. We hypothesized that this symbiosis is critical to enhanced millet growth in shrub
intercropping systems of the WAS which receive little inputs of synthetic fertilizer.

Therefore, we measured infection rates in the roots of millet growing adjacent to and far from the shrub as well as in the shrub itself. We also examined AM communities in the soil using fatty acid methyl esters (FAME) and spore morphology and found high levels of colonization at all four sites with the highest levels in the drier Sahelian zone.

Likewise, FAME analysis showed greater AM soil communities in this northern drier region. Compared to previous studies, spore densities were larger both near and far from *G. senegalensis*. In addition, we found thirteen AM species previously-unrecognized in the WAS. Overall, this study lays the foundation for future AM mechanistic studies and shows the importance of this symbiosis in the region.

Chapter 5 is a literature review of the ecology, management, benefits, socioeconomic implications, and agroforestry potential of shrubs in the WAS. In total, twenty-eight species are described in the review. Most of them were the dominant woody vegetation in the region, and the study showed that they have excellent potential for agroforestry systems that can increase food security. *G. senegalensis* and *P. reticulatum* in particular possess morphological and physiological traits that make them very well-suited for wide-scale agroforestry across the region. This review characterizes new research avenues for shrubs and is the first to examine this subset of the woody vegetation as distinct from trees.

Overall, this dissertation adds to the scientific knowledge on shrubs in the Sahel. It can further be used to guide shrub-based agroforestry research in other dryland regions of the globe. The results clearly indicate the importance, efficacy, and potential of native shrubs for increasing food security in the WAS.
For the people of the West African Sahel with eternal gratitude for all you taught me.
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For a boy who never even planned on going to college, these past 6 years of graduate school have been quite an adventure. I wouldn’t have wished it any other way and am deeply grateful to my advisor, Richard Dick, for taking a chance on me and facilitating every step of this journey: academically, financially, and professionally. From the beginning, he told me, “This is not Harvard, Matt; you’re here to get an education.” I hope I’ve lived up to his expectations and have taken every opportunity for growth that presented itself.

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Vita

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Preface

*Scientia potentia est* – Sir Francis Bacon

On 22 April 2017, in six hundred ten cities across six continents a singular event occurred, perhaps unprecedented in the history of the world – hundreds of thousands of people took to the streets purportedly to express nothing more than their support for and celebration of the organized pursuit of knowledge. The event was straightforwardly called the ‘March for Science’ with a mission to champion “robustly funded and publicly communicated science as a pillar of human freedom and prosperity¹.” While marches inspired by science and seeking to effect policy decisions have frequented the pages of history – the large 1982 march against the proliferation of nuclear weapons an example – the March for Science was something exceptional. It was a worldwide demonstration for a concept, a process, and a system to discover truth. If our times can be called unique, it is the degree to which we understand that current challenges facing humankind are interconnected and span the globe.

Rising surface temperatures, rising sea levels, and increasing human population, all in conjunction with simultaneously decreasing renewable resources, are challenges facing the entire planet. More than ever, we now keenly understand that the root of these

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¹ [https://www.marchforscience.com/mission/](https://www.marchforscience.com/mission/)
challenges is at least as much environmental as socioeconomic. We now understand that world peace and sustainable economies are built on proper care for the earth, our common home. In this way, it was fitting that the March for Science occurred on Earth Day, and as one of the principal March for Science slogans read, “There is no Planet B.” The question that must be answered by each of us as individuals, as nations, and as a planet is what processes should be used to address global challenges? While the peoples of the world are clearly divided by differences in religion, culture, language, economics, and politics, the system of ‘science’ transcends those boundaries with only one objective—to understand how the world works. In this way, scientia potentia est—or knowledge is power. This dissertation is simply one small example of how science can be used to help illuminate and improve a global challenge – that of food security, and specifically, food security in the West African Sahel.
Chapter 1: Food Security in the West African Sahel: A Challenge for Our Times

The global food security challenge: Historical context

Engraved in granite on the walls of the Franklin Delano Roosevelt Memorial in Washington, D.C., are four freedoms¹ which the 32nd president of the United States declared to be “essential” for everyone “everywhere in the world” (Roosevelt, 1941). The backdrop of President Roosevelt’s 1941 State of the Union Address, where he made this stirring proclamation, was a United States on the brink of war and besieged by threats both from within and without. His tone was surprisingly optimistic. The war to be fought (if it must be so) would be fought to secure not only American freedoms but also human freedoms. The new postbellum world which President Roosevelt sought to usher in would be one free from want. Remarkably, the president continued that this world would be “attainable in our own time and generation.” What is extraordinary about this address is Roosevelt’s singular vision – that the security and interests of his own country were intertwined with those of the world, that the fates of nations were inextricably bound together, and that with global unity came shared global responsibility. The newfound responsibility that Roosevelt alluded to was that of ensuring that humans everywhere in the world were free from want. As an affirmation of President Roosevelt’s

¹ Freedom of speech, freedom of religion, freedom from want, freedom from fear.
insight, “freedom from want” was subsequently adopted by the United Nations (UN) as a founding principle and raison d’être in its Declaration of Human Rights (General Assembly Resolution 217A).

Seventy-six years after Franklin Roosevelt uttered his famous words, the world has still failed to achieve freedom from want. For many people the concept is merely hypothetical. Particularly disconcerting is the lack of basic food security across the globe. Defined by the Food and Agriculture Organization (FAO) of the UN, food security occurs “when all people, at all times, have physical, social, and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life” (FAO, 2009). In a large survey of 134 countries with 124,000 participants (close to 1,000 participants/country), Smith et al. (2017) found that 27% of the respondents were food insecure, and in countries with low-income economies (making <$1,045 per capita annually), that proportion was 50% of the population. The FAO puts the number of undernourished (those with an insufficient daily calorie intake) at 795 million globally (FAO et al., 2015).

Although freedom from want for all people everywhere in the world has yet to be obtained, substantial progress has been made. The number of the undernourished around the globe has decreased by 216 million from the early 1990s to 2015 (FAO et al., 2015). In developing regions across the world that reduction represents a decrease from 23 to 13 percent of the total population. The lessening of hunger is a considerable achievement considering that the world’s population increased by 121% from 1965 to 2015 (FAOSTAT, 2017). A major reason for the decrease in the numbers of undernourished during a time when the total population increased by 121% was that global yields grew
for the staple crops rice (by 117%), soybeans (by 130%), wheat (by 166%), and maize (by 182%) during those same years (FAOSTAT, 2017). Furthermore, global food prices also decreased and then plateaued in the 1980s and have stayed relatively flat since then (Godfray et al., 2010).

The global food security challenge: Present and future constraints

Nevertheless, certain indicators portend an uncertain future for a world free from want. The global population continues to rise and is expected to reach 9 billion by 2050 (Godfray et al., 2010). Rising incomes across large portions of the globe are leading to increased animal protein consumption (Keyzer et al., 2005) which is a far less efficient means for supplying gross calories per hectare of land. Even in regions with relatively low levels of per capita meat consumption, globalization is fueling changes in carbohydrate dietary preferences which puts a strain on food security. An example is Africa where currently there is a shift away from the traditional dietary staples cassava, sweet potatoes, and maize towards rice, which is much more resource-intensive and difficult to produce (Ravn, 2014). In addition, relying primarily on one staple grain to fill most caloric needs also poses a threat to food insecure regions where events such as the quadrupling of the price of rice in the space of several months during the 2008 global recession fueled a mini food crisis. The volatility in commodity crop prices is also exacerbated by increasing demand for their use as biofuels (Pickett et al., 2008), which might further elevate future food prices.

Though the amount of land devoted to agriculture grew by approximately 9% from the 1950s until the early 2000s and now occupies about 38% of Earth’s land surface
(Foley et al., 2011; Pretty, 2008), the prospects for increasing arable land are slim (Erb et al., 2016; Garnett et al., 2013). In fact, in the last thirty years much agricultural land has already been lost due to human land-use management or mismanagement decisions such as urbanization, salinization, erosion, and desertification. These losses will probably increase (FAO & ITPS, 2015; Nelleman, 2009).

The final major threat to a future world free from want is climate change (Wheeler & Von Braun, 2013). For the staple crops maize and soybeans, yields diminish rapidly each day where temperatures are >30ºC (Schauberger et al., 2017). Consequently, most future scenarios predict greater frequencies of higher temperatures across the globe which will severely affect global crop productivity (Chung et al., 2014; Coumou & Rahmstorf, 2012).

To overcome these formidable obstacles and to attain lasting global food security is a daunting task. Studies suggest that the world will need to produce 60 to 110% more food than the current levels by 2050 to achieve the FAO’s definition of food security for all peoples across the globe (Alexandratos & Bruinsma, 2012; Pugh et al., 2016). Recognizing the scope of this herculean task, the former UN Secretary General, Ban Ki Moon, launched the Zero Hunger Challenge in 2012, with the goal to eliminate hunger during this generation (Ban, 2012). The Secretary General declared this to be a “challenge for our times,” a sentiment that has been reiterated by other leading scientists and institutions (Foley et al., 2011; D. P. Garrity et al., 2010; MEA, 2005). The Zero Hunger Challenge was furthered solidified as a policy agenda in 2015 with the introduction of the second UN Sustainable Development Goal, which calls for “ending hunger and achieving food security for all people by 2030.” (United Nations, 2015).
However, considering the likelihood of all the regions of the world to achieve a sustained food security, sub-Saharan Africa (SSA) might prove to be the Zero Hunger Challenge’s greatest challenge.

*Food security challenges in sub-Saharan Africa*

Much of the disparity in food security between SSA and the rest of the world can be traced back to post World War II advances in agricultural technology which took root unevenly in many developing regions of the world. During the mid-20th century, scientists worked assiduously to breed high-yielding cultivars of the staple crops wheat and rice. This scientific enterprise transformed agriculture in Central America and Asia in a collective effort known as the Green Revolution. The objective of the plant breeding efforts led by Dr. Norman Borlaug, the Father of the Green Revolution, was twofold: 1) to make plants disease-resistant, and 2) to adapt them to large quantities of fertilizer by eliminating the age-old problem of lodging (the historical outcome of too much fertilizer application), which occurs when plants respond to high nitrogen (N) levels by growing very tall, developing thin stems, and then falling over under the weight of seed heads. The semi-dwarf cultivars developed by Dr. Borlaug and other scientists reshaped agriculture in areas of the world that were able to adopt them. Then, seemingly unlimited quantities of inorganic fertilizer could be used on staple crops without adverse effect. Not surprisingly, fertilizer use exploded across the world; and especially in East Asia, yields more than quadrupled since the 1950s and now average 4.5 Mg ha\(^{-1}\) for the grain crops (Gilbert, 2012). As a result, new farming methods and technologies were developed around the increased use of inorganic inputs and these high-yielding cultivars.
Due to many and complicated factors, SSA largely did not benefit from the Green Revolution – either from the use of cultivars, fertilizers, or technology – and as a result grain yields in the region largely stagnated and still remain at an average of 1 Mg ha\(^{-1}\) (Gilbert, 2012), less than a quarter of global yields. The average fertilizer use across the region is 8-10 kg ha\(^{-1}\) (Garrity et al., 2010; Gilbert, 2012) which accounts for less than 3\% of global usage. While total yields increased some in SSA over the past half century, most of that was attributable to the expansion of cultivated land (Challinor et al., 2007). Furthermore, the low increases in yields coincided with an African population that more than quadrupled from 1950 to 2015 – from 229 million to 1.19 billion (FAOSTAT, 2017). The population explosion, coupled with poor yield growth, meant that between 1970 and 2000, per capita food production actually decreased by nearly 20\% across the continent (Abdulai et al., 2004). The consequence is that today, while 13\% of the global population is undernourished, in SSA 23\% of the population (218 million people) is undernourished (FAO, 2015).

The lack of agricultural productivity, however, belies the importance of farming to African livelihoods. Close to one third of the GDP of SSA stems from agriculture (World Bank, 2008), and 70\% of the African labor force is employed in jobs related to it (Garrity et al., 2010). Furthermore, approximately two thirds of livelihoods across the continent are derived from agriculture. While yields across the continent are small, farm sizes are equally small. Eighty percent are less than two hectares (Garrity et al., 2010). Though the land itself is a farmer’s greatest asset – the regenerative force that sustains

\(^{3}\) In Western Europe and East Asia, average fertilizer use is >200 kg ha\(^{-1}\) (Breman et al., 2001).
them – in Africa this natural gift is fraught with tremendous challenges. Less than 10% of the continent is considered prime farming land (Eswaran et al., 1997), whereas approximately 65% of Africa’s land is considered degraded (Bationo et al., 2012). Soil fertility is extremely low in SSA where 80% of the total arable land is considered seriously nutrient-deficient or has major physical constraints to production (AGRA, 2014). Lal (2004) found that the annual depletion rate of N, phosphorus (P), and potassium (K) from cultivated lands in SSA that lacked fertilizer inputs was estimated to be 40 kg ha\(^{-1}\) since the 1960s. In total, 7,270 Mg of soil nutrients, which are worth nearly US $4 billion, are lost annually from the region (Sanchez and Swaminthian, 2005; Toeniessen et al., 2008; AGRA, 2013). Of all the regions of SSA with perhaps the most constraints for the sustainable production of sufficient, safe, and nutritious food, the Sahel is conspicuous for the extreme challenges posed by its environment and socioeconomic conditions.

**Environmental challenges in the West African Sahel – Climate**

The African Sahel – derived from the Arabic *Sahil* meaning ‘shore’ – is a semi-arid\(^4\) ecological transition zone between the arid Sahara Desert in the north and the tropics of the South. It forms a band of land 400 to 600 km wide from approximately 12 to 18\(^\circ\) north latitude that stretches over 5,000 km from Senegal in the West, to Eritrea in the East (Le Houerou, 1980). The boundaries of the region are more specifically defined by rainfall isohyets; the northern extent receives 100-200 mm yr\(^{-1}\) while the southern

\(^4\) Where precipitation is less than potential evapotranspiration.
limit receives 600 mm yr\(^{-1}\) (Anyamba & Tucker, 2005). The natural vegetation and ecology of the Sahel is distinctive of semi-arid regions, and the ecosystem is typically either grasslands or savanna\(^5\) – a mixture of scattered trees and shrubs with grasslands.

In keeping with its identity as a transition zone, i.e. a region typified by natural change in flux, the Sahel has experienced significant climatic variation over the past 120 years since rainfall measurements have been measured. Across the West African Sahel\(^6\) (WAS), the two major weather events – a 7-8 month dry season followed by a 4-5 month rainy season – have been traditionally understood to be controlled by the oscillations of the Intertropical Convergence Zone (ITCZ)(Nicholson, 2001). This low-pressure area moves north away from the equator during the summer rainy season (June to October) inducing a monsoon with heavy storms and high-volume rainfall episodes. Rainfall intensities >100 mm hour\(^{-1}\) are not uncommon in the Sahel (Hoogmoed and Stoonsnijer, 1984). During the fall months, the ITCZ retreats southward, and between December and March a high-pressure band over the Sahara causes a dry northeasterly trade wind called the Harmattan to blow over the WAS. These winds are frequently laden with Saharan and Sahelian dust which have been covering the WAS for millennia. New research suggests that the ITCZ model is an oversimplified paradigm and that the weather patterns controlling the West African monsoon involve the thermodynamic contrasts between the

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\(^5\) The official definition of ‘savanna’ is an ecosystem of mixed grasslands and trees where the trees are spaced far enough apart so that the canopy does not close.

\(^6\) For the purposes of this dissertation, the West African Sahel includes the countries of the Sahel which are also described by the FAO as being in West Africa: Senegal, Mauritania, Mali, Burkina Faso, Niger, and northern Nigeria.
Sahara and the Atlantic, the interaction of jet streams, shear zones, and low pressure areas (Nicholson, 2013).

Throughout the 20th century, the WAS was subject to the most protracted decreases in rainfall of any region of the continent (Nicholson, 2001). The first 20 years of the last century were characterized by below average rainfall in the WAS followed by good conditions during the 1920s and 30s. The 1940s saw uneven rainfall with some drought years and some wet years. The 1950s was a wet decade where every year had above average rainfall, and the sufficient rainfall lasted through the mid 1960s. However, from the late 60s to the end of the century, a protracted period of aridity descended over the WAS. Every year from 1970 to the late 90s was anomalously dry (Nicholson, 2000), and the region was affected by severe droughts in the 1970s and 1980s with an especially devastating year in 1984 (Roehrig et al., 2013). Particularly disastrous was the fact that the drought covered the whole of West Africa (an area of 6,000,000 km²) with average rainfall of 190 mm over that 20-year period, whereas the annual rainfall from 1950-1969 was 300-400 mm (Lebel & Ali, 2009). The droughts of the 70’s and 80’s were catastrophic for the region, precipitating famines and migrations and contributing to poor economic growth (Lebel & Ali, 2009; Stige et al., 2006).

The past 20 years have seen an increase in rainfall (Hänke et al., 2016; Roehrig et al., 2013), but levels are still below the average rainfall of 1950-1969 (Lebel & Ali, 2009). As recently as 2011, a drought in Niger put 5 million people at risk of hunger. Moreover, in recent years there has also been a higher frequency of more extreme weather events such as droughts and floods in the WAS (Descroix et al., 2012; Lebel & Ali, 2009; Roehrig et al., 2013). These extreme events in the WAS are only expected to
increase and be exacerbated by climate change (Dai, 2013; Xue et al., 2016). The international consensus of the high probability of future climate challenges for the region was solidified by a report from the Intergovernmental Panel on Climate Change (IPCC), which predicts long and intense future droughts for the region (IPCC, 2012).

Debate over the past half century has centered around the role that humans play in inducing droughts and consequent land degradation\(^7\) in the Sahel. The concept of land degradation has historically been closely linked to that of ‘desertification’\(^8\) – essentially land degradation in dry areas – which has been used to describe landscape dynamics across the WAS during times of drought. In the 1930s, the British forester, Edward Percy Stebbing, was one of the first authors to publish the conclusion that the Sahara Desert was encroaching southward into the Sahel and that the cause of this expansion was from human activity (Stebbing, 1935). Thus, the concept of desertification took on a literal meaning as that of an “advancing desert”\(^9\).” However, with the mid-20\(^{th}\) century increases in rainfall concerns about desertification receded.

A reversal of collective thought occurred in the 1970s and 1980s with the onset of increasing aridity. Human-induced, irreversible desertification from overuse of the land became the predominant paradigm used to understand the overall vegetation losses in the region (Charney, 1975; Sinclair & Fryxell, 1985; UNCOD, 1977). One author, Lamprey (Lamprey, 1975) concluded that the problem was so severe that the Sahara Desert had

\(^7\) Defined here as the loss of terrestrial ecosystem productivity leading to the sustained loss of natural vegetation or crop yields.

\(^8\) Defined by the UN Convention to Combat Desertification (UNCCD) as “land degradation in arid, semi-arid and dry-humid regions resulting from various factors, including climatic variations and human activities.” (UNCCD, 1994 #557)

advanced permanently southward by 90-100 km in parts of Sudan between 1958 and 1975. The difficulty with proving the assertion that desertification was an irreversible, anthropogenic process lay in the fact that climate variability was often not considered as a controlling variable in the process. To use the example of Lamprey’s study, between 1958 and 1975, rainfall declined by almost 50% across the Sahel, yet that salient fact was not considered as a potential primary cause. Nevertheless, the fear of human-induced, irreversible desertification came to affect global policy decisions. In 1977, the UN approved a *Plan of Action to Combat Desertification* at its first ever Conference on Desertification held in Nairobi (Mortimore & Turner, 2005). In 1992, the UN held another significant meeting, the Convention to Combat Desertification (CCD), in which >150 countries ratified National Action Plans to halt the pernicious threat. Unfortunately, many of the policy strategies to reverse degradation failed because they did not take into account the effect of declining rainfall on vegetation decline. Thus, the recommended technologies were unsuitable for the reduced rainfall (Mortimore & Turner, 2005).

Recent research has shown that the long-term boundary of the Sahara Desert has not changed (Nicholson et al., 1998), and that oscillations in the degree of desertification are in fact controlled mainly by climate variability with vegetation making a recovery when rains return after drought (Anyamba & Tucker, 2005; Brandt et al., 2017; Reynolds & Smith, 2002; Tucker et al., 1991). Over the past 20 years the Sahel has experienced a ‘re-greening’ with an overall increase in vegetation\(^\text{10}\) (Brandt et al., 2015; Dardel et al., 2014; Kaptué et al., 2015). Despite the trend of expanding vegetative productivity,

\(^{10}\) These increases are determined by satellite measurements using normalized difference vegetation index (NDVI) data.
desertification nonetheless remains a constant challenge and pernicious threat to food security in the region. This is because the Sahel is an especially fragile environment where humans are heavily dependent on the interaction between the natural vegetation, soils, animals, and climate to sustain livelihoods. Consequently, though rainfall can increase at the regional scale with an ensuing increase in overall vegetation, at a localized scale, human-induced pressures and changes to the landscape have a large effect on either inducing, containing, or reversing desertification (Herrmann et al., 2014; Herrmann & Tappan, 2013; Mortimore & Turner, 2005; Rasmussen et al., 2001). Therefore, the main reason for desertification in the WAS, even during a time of re-greening, is an overexploitation of the natural resources of the land (Breman, 1992), stemming from intensive agriculture and animal husbandry which then leads to soil nutrient losses and erosion. In total, the extent of severely degraded soils across the region that have resulted from agricultural activities has been estimated at 1.1 million km$^2$ (Vägen et al., 2005).

Environmental challenges – Soils

Land degradation poses an extreme challenge to food security in the WAS, not only because of climate (previously discussed) and the fact that a majority of the population depends on subsistence agriculture\textsuperscript{11} for livelihoods but also because the soils themselves are some of the oldest and most weathered in the world (Bationo et al., 1998; Lahmar et al., 2012). Da Costa et al. (2015) described it as, “one of the poorest and most environmentally degraded areas on earth.”

\textsuperscript{11} (Sterk, 2003) put that number at 85 to 90%.
The predominant soil parent materials\textsuperscript{12} over the northern region of the Sahel are eolian (wind-deposited) sands from the Sahara (Hoogmoed & Stroosnijder, 1984). Soils formed from these deposits have predominantly loamy sand textures (approximately 90% or more sand) to a depth of at least 100 cm, no diagnostic horizons other than an A or E horizon, and are classified as Arenosols by the FAO classification system (FAO, 1988). The other two main reference soil groups across the WAS are Lixisols and Acrisols (Da Costa et al., 2015) which are both classified by their diagnostic argillic B horizons with low cation exchange capacities (<24 cmol(+)/kg \textsuperscript{-1} soil) overlying a slowly permeable horizon. The difference between the two is that Acrisols have a base saturation of <50% in the top 125 cm of the soil, whereas the Lixisols have a base saturation of at least 50% throughout the horizon. Finally, over a smaller area of the WAS, there are also some Nitisols – soils with uniform levels of at least 20% clay in the argillic B horizon; Ferralsols – soils with high iron and sesquioxide concentrations and low base saturations, and; Plinthosols – soils with at least 25% plinthite by volume in a horizon \textgtr 15 cm thick within the top 50 cm of the surface.

Much of the soil formation in the WAS is related to erosion cycles that have occurred since Precambrian times with major parent material depositions in the Neogene and Quaternary periods (Herrmann & Sterk, 1996). Da Costa (Da Costa et al., 2015) classifies six major parent materials for the region from which soils formed in a north to southward direction: 1) Saharan sands and dunes; 2) Quaternary sands with their origin from the Niger River; 3) Mixed sands and clay-sands from the Neogene period that

\textsuperscript{12} The materials from which the soil forms.
underwent significant weathering; 4) Cambrian to Ordovician sandstones in Mali and Burkina Faso; 5) crystalline igneous and metamorphic rocks, and 6) coastal sediments. In relation to landscape position, Stroosnijder (Stroosnijder, 1982) describes three main types of soil/relief combinations in the WAS: 1) Across 50% of the landscape area, deep sandy soils occur either as dunes or eroded dune fields; 2) Shallow stony soils over laterite or sandstone cover 30% of the landscape, and 3) Deep clay soils occupy the remaining 20% of the land area.

Overall, these soils present a difficult challenge to agricultural productivity. Unlike most continents, Africa did not receive infusions of soil nutrients from relatively recent (in geologic time) glaciation or volcanic activity. Consequently, the parent materials from which the soils form severely constrain fertility. The sands that cover much of the WAS are predominantly quartzite (SiO$_2$) and thus do not contain most of the nutrients needed by plants. Theses soils further constrict fertility because sand particles have a low surface area, are not colloidal, and mostly do not participate in the cation exchange capacity (CEC). Furthermore, the sands frequently form thin surface crusts which reduce infiltration into the soil (Hoogmoed & Stroosnijder, 1984). Another physical challenge resulting from deep sandy soils is the high prevalence of nutrient leaching (Da Costa et al., 2015) and also a low water holding capacity for use by plants compared to soils with higher percentages of clay and silt. Erosion by both wind and water is a constant threat and is responsible for the removal of much of the fertile surface soils in the Sahel (Breman et al., 2001). The sandstones which underlay a lot of the sands and form the parent material of other soils are acidic and contribute to aluminum (Al$^{3+}$) toxicity in some regions of the Sahel (Lahmar et al., 2012). Soils with laterite clays and
gravels in the WAS often form hardpans that restrict root growth and water infiltration (Da Costa et al., 2015), and those soils with plinthite are very difficult to cultivate at all. Finally, because of prevailing high temperatures and aridity, there is very little organic matter in Sahelian soils (Bationo et al., 2007; Breman et al., 2001; Da Costa et al., 2015). Soil organic matter (SOM) plays a central role in physical, chemical, and biological processes in the soil which together increase the productivity of the land (the opposite of desertification). Within limits, SOM can also be controlled by management. Consequently, its low levels in most soils of the WAS is one of the root causes of food insecurity, and any attempt to increase yields must first increase SOM.

*Environmental challenges – Vegetation*

The WAS is predominantly a rare ecosystem in which humans preserve the natural savanna ecology but modify it to meet the demands of subsistence lifestyles. More frequently, however, humans view natural landscapes and managed landscapes as distinct from one another. To solidify the boundaries, we give names to the natural lands such as ‘national parks’ and ‘wilderness areas.’ The same is true for managed lands. Consequently, we call lands cleared for agriculture, ‘fields.’ Lands for fruit production we describe as ‘orchards.’ Lands for animal husbandry we know as ‘pasturelands.’ Moreover, the traditional attitude, which is seemingly ingrained in our psychology, is that nature is a force to be subdued. Ergo, we clear the land. We fish the seas. We log the forests. These time-honored practices are spoken of with reverence.

Due to the natural constraints of climate and soil, and because there is very little mechanized agriculture or investment in fertilizers and other inorganic inputs, the
denizens of the WAS work in conjunction with their environment to sustain livelihoods. At the center of these interactions is the woody savanna vegetation ubiquitous across the landscape. The mixture of trees and shrubs across the Sahel provides an average of 7% canopy cover over the soil surface at the 1 km scale (Brandt et al., 2016). The canopy cover increases with rainfall in a north to south direction from roughly 2 to 15%.

Farmers have been working to integrate trees with crops and livestock for generations in order to sustain their livelihoods against the inherent environmental challenges of the Sahel (FAO, 2011; Neufeldt et al., 2012). Thus, woody vegetation has remained at the center of the ecological landscape, but the specific species found today are the result of human selection over many generations (Boffa, 1999; Van Noordwijk & Ong, 1999). Thus, the Sahel has been referred to as a ‘cultural landscape’ (Rasmussen et al., 2001).

The system of agriculture where farmers grow crops and herd livestock among managed trees and shrubs is known as parkland agroforestry, and the areas themselves with crops growing among selected and maintained woody perennials are called parklands. Though parklands are found in Southern Africa and the Mediterranean, the largest parklands in the world are in the WAS (Zomer et al., 2009).

The woody vegetation of the WAS provides important ecosystem services, which are classified as provisioning (food, medicine, animal fodder, construction, fuel), regulating (water purification and climate change mitigation), supporting (soil fertility improvement, soil building, erosion prevention), and cultural (historical, spiritual, aesthetic) (Bayala et al., 2014; Sinare & Gordon, 2015). Research on parkland

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13 Defined as the benefits people receive from ecosystems (MEA, 2005).
agroforestry ecosystem services in the WAS began relatively recently, and few papers were published on the subject before the early 1990s (Sinare & Gordon, 2015). Most of the research in parkland agroforestry systems, however, has focused on trees, with shrubs considered as an afterthought or sometimes not at all (Bayala et al., 2015; Garrity, 2004; Garrity et al., 2010; Sanchez, 1995). Lufafa et al. (2008a) noted that the potential of shrubs to provide ecosystem services has largely been overlooked.

Recent studies, however, suggest that the re-greening of the Sahel has coincided with decreases in both alpha and beta diversity of tree species but concurrent increases in the number of woody shrubs (Maranz, 2009; Gonzalez et al., 2012; Herrmann & Tappan, 2013; Hänke et al., 2016; Brandt et al., 2017). Moreover, the consensus is that human management practices and selection – especially pressures from increased cropping and animal husbandry – are responsible for much of the tree declines (Hänke et al., 2016; Herrmann et al., 2005; Larwanou & Saadou, 2011; Rasmussen et al., 2014). The overall ‘re-greening’ of the Sahel, therefore, might in effect be an increase in the density of native shrubs while tree species declined.

One of the most ubiquitous and dominant shrub species with documented increases across the WAS is Guiera senegalensis J.F. Gmel (Brandt et al., 2017; Issoufou et al., 2013; Seghieri et al., 2005). Another dominant shrub across the Sahel is Piliostigma reticulatum (DC), Hochst (Diaack, 2000; Yelemou et al., 2009). These two shrubs are known and used by inhabitants of the Sahel for fuel, construction, animal fodder (only in the case of P. reticulatum), and medicine, (Arbonnier, 2004; Wezel, 1999; Yelemou et al., 2009). Recently, some research has focused on their ability to improve soil quality and crop yields (Dossa et al., 2009, 2012, 2013; Kizito et al., 2007; Lufafa et
al., 2008b). However, the long-term potential of these shrubs to improve yields in parkland agroforestry systems has not been studied.

Socioeconomic challenges to food security

The population of the WAS is growing by approximately 3% per year (FAO, 2014), and estimates are that 29 million people of the Sahel’s total population of 135 million\textsuperscript{14} are food insecure (FAO, 2014). The threat is especially pernicious in West Africa where at least 40% of the population is younger than 15 years of age.\textsuperscript{15} Children in developmental stages are disproportionately affected by undernourishment with permanent effects on physical and mental health. At the same time that the population is exploding, crop yields in the region are increasing at about 1% per annum (Chauvin et al., 2012; FAO, 2014). The result of the growing population and low yield growth is that the area of land under cultivation in the WAS has increased rapidly in recent decades (especially in Niger) which has strained the natural ecosystem that is so vital for increasing yields in the Sahel (Cappelaere et al., 2009).

In addition, the population increases are conjoined to extreme socioeconomic constraints to yield improvements in the Sahel. The first is that the price of inorganic fertilizers and other external inputs are higher than in most regions of the world. There are two reasons for this (Breman et al., 2001). The primary one is the prevalence of diffuse small farms across the region with low crop densities, nullifying economies of scale and making transport and supply costs inordinately expensive (The road density of

\textsuperscript{14} Population statistic from (Haub & Kaneda, 2014).
\textsuperscript{15} In the United States, 21% of the population is 16 or younger.
West Africa is one tenth of that found in Southeast Asia.). The second is that fertilizer use is very inefficient in the WAS because it occurs mostly on degraded lands. As a result, fertilizer use is largely ineffective without concurrent organic inputs to increase soil carbon (Ibrahim et al., 2015). Breman et al. (2001) proposed other socioeconomic constraints for yield improvement which include: 1) A lack of national policies to control market prices and keep crop prices from collapsing after harvests; 2) national policies that keep food prices low in order to benefit consumers over producers; 3) a deficiency of policies to stimulate private sector investment in markets for both agricultural inputs and products; 4) very low access to credit to improve agricultural knowledge and technology; 5) unequal access to land, credit, and agricultural training among the population which is especially apparent in gender gaps between male and female farmers.

The final barrier to agricultural economic advancement in the WAS is the lack of significant investment in breeding high yielding cultivars for the staple crops that can grow in this region (Jukanti et al., 2016). In contrast, over the past 80 years, one of science’s greatest achievements has been the extraordinary research effort and success in improving the high-value staple crops – maize, rice, wheat, and soybeans – which is in large part responsible for the enormous yield gains during this time. Nevertheless, at present there is little incentive for businesses in the private sector to turn their research efforts towards developing high-yielding varieties of pearl millet, sorghum, groundnuts, and cowpeas. Even if high-yielding varieties were developed that could overcome the many abiotic and biotic constraints of the WAS, they would still have to be heavily subsidized in order to be adoptable by subsistence farmers. In the case of maize, for example, which is one of the most intensively-researched plants on the planet with many
high-yielding varieties, more than 50% of the land area planted to it in the developing world is still done with unimproved varieties (Shiferaw et al., 2011).

Conservation agriculture for food security

Overcoming the environmental and socioeconomic constraints to food security in the WAS requires improving soil quality by using the biological resources of the region to increase yields of the two crops: pearl millet (*Pennisetum glaucum* (L.) R. Br.) and groundnut\(^1\) (*Arachis hypogaea* L.). Across the Sahel, these two crops are the backbone of livelihoods. Pearl millet is a staple crop, and groundnut is a cash crop grown for export and to improve soil fertility in rotation with millet (Mason et al., 2015; Stoate & Jarju, 2008). In Niger, these two crops were harvested from 57% of the country’s arable land in 2014, and for Senegal, Mali, and Burkina Faso, they were harvested from 49, 37, and 32% of harvested lands respectively (FAOSTAT 2017). The Sahel urgently needs scientifically-validated agricultural systems to guarantee landscape conservation, to provide sufficient and sustainable nutrient and water supplies, and to optimize productivity for these two crops. These goals also align with two of the five specific objectives of the UN’s Zero Hunger Challenge, which are: 1) “To make all food systems sustainable,” and 2) “To generate a 100% increase in small holder productivity and income” (Ban, 2012).

Much recent research has focused on conservation agriculture (CA) practices that have potential to increase yields across the whole of SSA and the WAS in particular.

\(^{16}\) Referred to as ‘peanuts’ in the United States.
(Bayala et al., 2012; Lahmar et al., 2012; Mason et al., 2015; Scopel et al., 2012). These practices rely on using local resources to improve soil fertility and water conversation. Examples are: using post-harvest crop residues to cover the surface of the soil and increase soil moisture, or planting seeds with manure and other organic inputs, or growing mixed crops (e.g. cowpeas next to millet), and planting crops next to trees in agroforestry systems. These CA strategies are adapted to the region because they rely on readily available resources which cost little. Crop residues and animal manures, for example, are noted as the most available nutrient sources in cereal cropping systems of the Sahel (Bationo et al., 2007; Ibrahim et al., 2015). Unfortunately, although many of these CA practices improve yields, they are often not implemented because of socioeconomic constraints (Giller et al., 2009), or because the proposed inputs have more value in a management strategy that is mutually exclusive to the proposed CA strategy (Mason et al., 2015; Valbuena et al., 2015), or because the CA practice improves yields only under very specific environmental conditions\(^{17}\) (Bayala et al., 2012). Though many of the CA practices are not implementable, the tenets of the CA ideology are sound – using local, available resources to increase soil organic matter (SOM) which improves both soil fertility and moisture. Consequently, the challenge for researchers is to discover or develop CA practices that are truly implementable for the WAS.

\(^{17}\) See the introduction of Chapter 2 for more discussion of why CA practices are not implemented.
Increasing food security in the West African Sahel using native shrubs: Dissertation objectives

Thirty-eight years ago, a paper appeared in the scientific journal, Nature, entitled “Agroforestry: new hope for subsistence farmers” (Spurgeon, 1979). For the first time, research that focused on growing crops next to trees was placed in the global spotlight. In subsequent decades, much agroforestry research in SSA focused on the powerful effect that the so-called “fertilizer tree,” Faidherbia albida\(^{18}\), had on improving yields of crops growing under its canopy (Garrity et al., 2010; Sanchez, 1995). Though research into the parkland agroforestry systems of the WAS has shown that growing crops next to some trees can improve yields in certain situations, reviews on the subject suggest that \textit{F. albida} is one of the few trees with a consistently positive effect (Bayala et al., 2012, 2014, 2015; Sinare & Gordon, 2015). The reason for this is that there is frequently a lot of competition for sunlight\(^{19}\), water, and nutrients between trees and crops with the result that trees often have a negative effect on crop yields. It is equivocal whether trees are a viable CA practice for major yield improvement in the Sahel. Furthermore, a major concern for the future of tree-based parkland agroforestry systems in the Sahel is that the amount of cultivated land has increased rapidly in the past few decades because of continuous population growth (especially in Niger) which has caused a decline in the native woody vegetation (Cappelaere et al., 2009). Trees are more susceptible to population, cultivation, and drought pressures than native woody shrubs of the region like

\(^{18}\)Formerly known as \textit{Acacia albida}.

\(^{19}\)\textit{F. albida} has a reverse phenology; i.e., it loses its leaves during the summer growing season right before cropping begins and then leafs out during the winter dry season. Consequently, the tree is ideally suited for intercropping.
*G. senegalensis* (Gijsbers, 1994; Hänke et al., 2016; Herrmann & Tappan, 2013; Maranz, 2009). In summary, increasing shrub densities in the WAS, despite enormous environmental and anthropogenic pressures, suggests that future parkland agroforestry research should focus on the ability of shrubs to improve long-term yields.

This dissertation seeks to fill that research gap. The main objective is to understand the role of two native, dominant semi-evergreen woody shrubs, *P. reticulatum* and *G. senegalensis*, in improving soil quality for sustained yield increases of the two staple crops, pearl millet and groundnut, in the WAS. The overall hypothesis is that these shrubs are more effective at sustaining yields and increasing food security over the long-term than tree-based agroforestry systems because of their increased densities across the Sahel and because of their ability to withstand cultivation pressure. Further objectives are:

1) to determine if native shrubs can be cultivated as an agroforestry system over the long-term by increasing the densities of shrubs to approximately five times their native levels in the WAS and then growing crops interspersed within the shrubs;

2) to assess whether this increased-density shrub intercropping system is sustainable over the long-term, whether shrubs will experience a die-off after a certain number of years, and whether the shrubs will buffer millet and groundnut against drought;

3) to understand the ecology of how shrubs and crops seemingly do not compete with each other for limited nutrients and water;
4) to determine if the shrub and crop intercropping systems can offset carbon dioxide (CO₂) emissions by sequestering carbon in the soil over the long-term and consequently have potential for carbon credits;

5) to understand how *G. senegalensis* affects the communities of the beneficial symbiotic fungus, arbuscular mycorrhizal fungi (AMF), in the soil and AMF colonization rates both in the roots of *G. senegalensis* and in millet growing near the shrub and far from it;

6) to review and assess the literature on the ecology, uses, and potential of shrubs for agroforestry systems in the WAS.

It is the sincere hope of this author that the research and conclusions set forth in this dissertation will benefit the citizens of the WAS, advance sustainable food security throughout the region, and increase the breadth of scientific knowledge.

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2.1. Abstract

Throughout the Sahel, food insecurity remains a persistent threat. A few studies have shown that *Piliostigma reticulatum*, a dominant native shrub in parklands from Senegal to Sudan, can positively impact crop yields. However, there are no experiments that measure whether this species can stabilize long-term crop productivity under erratic rainfall. Therefore, an 11-year study of an optimized *P. reticulatum* intercropping system (1000 shrubs ha\(^{-1}\) with annual coppiced residue soil amendments) was initiated in 2004 in Senegal, West Africa to determine its impacts on crop productivity and soil quality. The experiment was a split-plot factorial design with the main plot shrubs (with and without) and the subplot fertilizer rate (0, 0.5, 1, and 1.5 times the recommended N-P-K rate) with an annual groundnut (*Arachis hypogaea*) and pearl millet (*Pennisetum glaucum*) crop rotation. Yield, biomass, soil carbon, and soil and plant nutrient data from 2011-2015 were compared with data from 2004-2007. The presence of shrubs increased millet and groundnut yield from 2011-2015 and rainfall water use efficiency (WUE) between 2004 and 2015. Without fertilizer addition, the shrub plots had approximately 2 times greater millet yield throughout the duration of this experiment. The presence of shrubs also

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improved soil quality, as evidenced by significantly greater C in the fraction <53 µm and total C in shrub over non-shrub plots. Thus, *P. reticulatum* intercropping promotes C sequestration. In addition, five macronutrients (N, K, Ca, Mg, S) and two micronutrients (Mn and Cu) were significantly greater in the shrub plots. The results provide strong evidence that intercropping with *P. reticulatum* is an ecological agroforestry system for the Sahel that can remediate soils, increase crop yields, and buffer climate change.

### 2.2. Introduction

Challenges abound for crop production in the Sahel—recurring drought, land degradation, sandy soils with poor natural soil fertility, low investment in crop breeding, and limited use of fertilizers (Bationo et al., 2007; Sultan et al., 2013; Epule et al., 2014; FAO and ITPS, 2015; Pucher et al., 2016). Most small-holder farmers rely on manure to maintain soil fertility, and across the continent the average fertilizer input is 8 to 10 kg ha⁻¹ which accounts for less than 1% of global usage (Garrity et al., 2010; Turner and Hiernaux, 2015). Thus, to address the challenges for food security in the Sahel, agroecosystems are needed that are ecological and use local resources.

Conservation agriculture (CA) practices (Bayala et al., 2012; Lahmar, 2012; Mason et al., 2015a) are frequently proposed to increase soil quality and crop yields. These include: 1) minimal or no tillage; 2) green manure; 3) mulching or maintaining soil cover; 4) diversified crop rotation; 5) planting crops under woody trees or shrubs. However, in a review by Bayala et al. (2012), there was high variability in the yield response associated with these practices across the Sahel, and most of them have limited
potential for wide-scale adoption. For example, in the case of mulching or manure, typically quantities are insufficient (Badiane et al., 2000) or the labor and time expenses are too great to be practical for the majority of subsistence farmers (Bayala et al., 2012). Moreover, crop or other residues frequently have greater value as animal feed, fuel or construction materials over addition to soils (Mason et al., 2015a; Valbuena et al., 2015). The use of green manures is dependent on sufficient rainfall (Bayala et al., 2012).

Woody vegetation improves soil quality, but often that does not translate into greater crop yields (Gnankambary et al., 2008; Bayala et al., 2012, 2015; Sinare and Gordon, 2015). In summary, in order for a CA technique to be implementable in the Sahel, it must not only improve yields but also be integrally connected to the ecology and socioeconomics of the region (Knowler and Bradshaw, 2007).

The Sahel is predominantly characterized by parkland agroforestry where farmers allow trees to remain in their fields interspersed with crops (Gijsbers et al., 1994; Bayala et al., 2014). One of the few common tree species that favors crop production is *Faidherbia albida* (Del.) A. Chev., because of its reverse phenology. However, it is slow growing, typically has low densities of 30 trees ha\(^{-1}\), and can take 4 to 6 years post-establishment before yields start to improve (Sanchez, 1995; Stoate and Jarju, 2008; Garrity et al., 2010). In recent years, more studies have focused on the CA potential of another component of parkland vegetation—native shrubs, and especially *Piliostigma reticulatum* and *Guiera senegalensis*. These shrubs are being studied as ecological and practical solutions for landscape remediation and the low yields of rainfed crops in the Sahel. Their advantages over trees are: higher densities, faster growth rates, limited competition for light, and prevention of erosion by entrapment of windblown sediment
leading to higher fertility soils (Geiger and Manu, 1993; Wezel, 2000; Seghieri et al., 2005; Leenders et al., 2007; Lufafa et al., 2008).

*P. reticulatum*, specifically, extends from Senegal in the west to Sudan in the east and the Democratic Republic of Congo in the south (Hernandez et al., 2015). Research has shown that this shrub has a significant effect on the hydrology of soils within its canopy influence by increasing volumetric water capacity, minimizing drainage losses by capturing water not used by crops, performing hydraulic lift (HL), and using water from deep in the soil profile thereby not competing for water used by crops (Kizito et al., 2006, 2007, 2012). This species also enhances rhizosphere microbiology increasing microbial biomass and respiration, arbuscular mycorrhizal colonization in adjacent plants, the diversity and composition of bacterial and fungal species (Diedhiou et al., 2009; Diedhiou-Sall et al., 2013; Hernandez et al., 2015). Furthermore, it promotes beneficial microorganisms, beneficial enzyme activity thereby increasing the rate of mineralization of nutrients for plant uptake, and overall biogeochemical cycling of phosphorus (P) and nitrogen (N) (Wezel et al., 2000; Dossa et al., 2008, 2013; Debenport et al., 2015; Diakhaté et al., 2016). *P. reticulatum* amplifies carbon (C) sequestration (Lufafa et al., 2008; Yelemou et al., 2013). Finally, in shrub-based cropping systems, pearl millet (*Pennisetum glaucum* (L.) R. Br.) and groundnut (*Arachis hypogaea* L.), yields are significantly increased in the presence of *P. reticulatum* (Geiger and Manu, 1993; Dossa et al., 2013; Debenport et al., 2015).

Both millet and groundnut are very important to livelihoods in the Sahel (Stoate and Jarju, 2008; Mason et al., 2015b). However, the long-term effects of *P. reticulatum* on their yields in addition to soil C and nutrient cycling have not been studied.
Moreover, it is unknown whether the shrubs can maintain yields over fluctuating year-to-year rainfall typical of the Sahel. The main objective of this study, therefore, was to determine if an optimized *P. reticulatum* and millet/groundnut intercropping system with shrubs at high densities could sustain or increase yields over an 11-year period. Auxiliary objectives were to measure the long-term effects of *P. reticulatum* on C sequestration and nutrient cycling between soil, shrubs, and crops.

2.3. Materials and Methods

2.3.1. **Experimental site**

This long-term *P. reticulatum* intercropping experiment is located near Nioro-du-Rip, Senegal, West Africa, in the southern Peanut Basin (13°45’N, 15°47’W), within the Northern Sudanian climatic region (Sarr et al., 2013). The elevation is 18 m above sea level with 0-2% slopes, and a savanna ecosystem predominates with trees and shrubs frequently growing together in farmers’ fields. The predominant shrub in this region is *P. reticulatum* with densities ranging from 134 to 288 shrubs ha\(^{-1}\) (Lufafa et al., 2008). *Piliostigma reticulatum* belowground biomass is characterized by a dimorphic growth pattern with > 90% of the root biomass found in a spreading pattern within 20 to 50 cm of the soil surface but anchored by a thick, woody tap root that branches and provides access to ground water (Kizito et al., 2006). Typically, the shrub crown height is 1 m high by 1 to 2 m in diameter and has multiple shoots. If left uncut, *P. reticulatum* can be found growing as a tree but maintains a shrub growth habit when coppiced regularly (Lufafa et al., 2008).
The soil is sandy (> 90% at the surface) has a 6.2 pH, and a loose consistency with very little horizon differentiation or clay. The FAO taxonomic classification is a fine-sandy, mixed Haplic Ferric Lixisol (Kizito et al., 2006). Air temperatures range from 20.0 to 35.7ºC and the mean annual precipitation from 2011 to 2015 was 709 mm which fell primarily between July and September (Fig. 2.1).

2.3.2. Experimental design

In 2003, a 0.5 ha field was selected to develop the long-term experiment that met the dual requirements of having established shrubs in place and having been managed under a yearly groundnut-millet rotation for at least 50 years until 2000, when it was fallowed for 3 years. The experiment had a randomized complete block split-plot design with the presence or absence of shrubs as the main plot and fertilizer rate as the sub plot (n=4). Eight main plots, 46 X 4.5 m, were established in the winter of 2003 where half of them had all shrubs removed manually (+shrub plots) and the other half used the existing shrubs and in most cases increased the numbers in each plot to achieve a shrub density ranging from 667 to 1555 ha⁻¹ (+shrub plots). Within each main plot, 4 subplots, 10 X 4.5 m, were established with a 2-m gap between subplots and a 3-m gap between main plots. Fourteen of the sixteen +shrub subplots had 4 or 5 shrubs subplot⁻¹, randomly but evenly distributed, representing a fixed density of either 889 or 1111 shrubs ha⁻¹ and thus an average density of 1000 shrubs ha⁻¹ across all +shrub plots. Data was collected from this experimental site for the years 2004 to 2007 and published by Dossa et al. (2013). The current study covers the years from 2011 to 2015. Other related studies that have been carried out at this site are Kizito et al. (2006, 2007, 2012) and Diakhaté et al. (2016).
During the summer of 2003, millet (var Souna 3) was planted in all plots and fertilized with 68.5 kg N, 15 kg P, and 15 kg K ha\(^{-1}\). The following year groundnut (var 77-33) was planted. Subsequently, the same varieties of millet (odd years) and groundnut (even years) were planted at the site until the end of 2015. Shallow pre-planting tillage and other practices were typical of the dominant farmer practices in the region (Dossa et al., 2013). Crop planting occurred each June with groundnut plants 15 cm apart with 50 cm between rows, and millet was planted at densities of 10,000 plants ha\(^{-1}\), 0.9 m X 0.9 m apart. During the cropping season, weeding was done by hand hoeing and with an animal-drawn shallow cultivator to a 5-cm depth. Beginning in 2004, the subplot fertilizer treatments were established. These were 0, 0.5, 1.0, or 1.5 times the recommended fertilizer rate for each crop. For groundnut, this was 9 kg N, 30 kg P, and 15 kg K ha\(^{-1}\) manually applied as a 6-20-10 blend post-germination and incorporated by hand hoeing to a depth of 5 to 8 cm. For millet, the recommended fertilizer rate was 22.5 kg N, 15 kg P, and 15 kg K ha\(^{-1}\) spread manually as a 15-15-15 blend and incorporated lightly by hoe at planting followed by a sidedressing of 46 kg N ha\(^{-1}\) as urea in 23 kg increments broadcast at 2 and 4 wk post-planting.

Each year, before the rainy season started in May or June, the shrubs were coppiced and cut into 5 to 10-cm pieces before these residues were spread evenly over the shrub plots. This stands in contrast to the current management of *P. reticulatum* in this region which consists of burning parts or all of the coppiced biomass prior to planting (Lahmar et al., 2012; Dossa et al., 2013). During the cropping season, shrubs were coppiced twice more per growing season and residues returned to soil surface. Shrubs regrew during the dry season when there was also no weeding of the plots. After
millet grain yield was harvested, the remaining millet biomass was left on the soil surface, but groundnut residue, which is typically harvested to feed livestock (Dossa et al., 2013), was removed from the fields. This sequence of management was maintained from 2004 to 2015 except that the fertilizer subplots were not kept up from 2008 to 2010 when no measurements were made.

2.3.3. Crop yield, WUE, biomass, and plant sampling

In October following crop maturity, the inner two-thirds of each subplot was harvested. For groundnut, the entire plant was dug up from each subplot, followed by 4 to 5 days of sun drying, before pods were removed from the biomass and each fraction was weighed separately. Millet grain yield was accomplished by harvesting panicles that air dried to <10% water content followed by separation of millet seeds from the panicle.

Water use efficiency (WUE) was calculated for both crops by dividing crop yield by annual rainfall—740, 900, 622, 720, 775, 964, 634, 513, and 658 mm in 2004, 2005, 2006, 2007, 2011, 2012, 2013, 2014, and 2015 respectively—to achieve kg yield ha\(^{-1}\) mm\(^{-1}\) rainfall. WUE was used to compare yields from 2004-2007 (published in Dossa et al., (2013)) with yields from 2011-2015. The aboveground millet biomass (leaves and stalks) was cut at the soil surface, weighed fresh, and a subsample of ~500 g was used to determine water content at 65°C. In 2015, representative samples of dried stems and leaves from each subplot were ground with a Wiley Mill to pass a 2-mm mesh and kept in sealed plastic bags for nutrient content analysis.

2.3.4. Aboveground shrub biomass and plant sampling

The fresh weight of aboveground shrub biomass was separated into leaf and stem components and recorded after each coppicing event. The shrub biomass was collected
in late spring (first coppice) and during the cropping season (typically two times).

Summing the biomass harvested over these two periods provided the annual shrub biomass yields. As with crop biomass fractions, a 500-g subsample of each component was used to determine moisture content. In 2015, representative fractions of dried stems and leaves from both shrub harvesting periods were ground and used to analyze nutrient contents.

2.3.5. Soil sampling

From 2012 to 2015, soil samples for chemical analyses were collected three times over the cropping season: 1) at planting but before fertilization (planting); 2) two months post-planting during the middle of crop growth (midseason), and; 3) at harvest. At each sampling, 10 soil cores (2.5 cm diameter and 0-10 cm depth) were randomly taken along diagonals within the inner two-thirds of each subplot. Soil samples were homogenized, air-dried, and sieved to pass a 2-mm sieve and a 200-g subsample kept in a sealed plastic bag at room temperature for further analysis.

2.3.6. Laboratory procedures

2.3.6.1. Soil carbon measurements

Total soil carbon was measured on a C-144 Carbon Analyzer (LECO Corp. St. Joseph, MI). Particulate organic matter carbon (POM-C) was determined on soils sampled at planting and harvest during 2012, 2013, and 2015, according to the methods of Cambardella and Elliott (1992). Briefly, 30-g soil samples were placed in 100 mL of a 5 g L\(^{-1}\) sodium hexametaphosphate \([\text{Na}(\text{PO}_3)_6]\) solution and dispersed by shaking for 16 h on a reciprocal shaker. The soil was then passed through a 53 \(\mu\)m sieve, rinsed, and the slurry passing through the sieve was dried until constant weight was achieved. The
samples were then analyzed for total C by combustion on the C-144 Analyzer. The difference between the C content of the slurry that passed through the 53 µm sieve and that of a duplicate undispersed soil was considered to be the POM-C >53 µm, whereas the C fraction of the dried slurry multiplied by the weight of the dried slurry was considered to be the C fraction <53 µm, and the summed fraction corresponded to the total soil C content. Bulk densities of 1.49 and 1.47 g cm⁻³ in the +shrub and -shrub plots respectively (Roger Bayala, personal communication) were used to calculate kg C ha⁻¹ to a 10-cm depth in +shrub and -shrub plots in 2015.

2.3.6.2. Soil nutrients

For 2014 and 2015 soil samples, plant macro nutrients: phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S); and micronutrients: manganese (Mn), iron (Fe), zinc (Zn), and copper (Cu) were extracted using a Mehlich 3 solution (ammonium-fluoride-EDTA) (Mehlich, 1984), followed by analysis on an ICP-OES 700 (Agilent Technologies, Santa Clara, CA)(USEPA, 2007). Total extractable inorganic nitrogen (N) in the form of ammonium (NH₄) and nitrate (NO₃) were analyzed on soil samples from 2014 to 2015. For the 2014 samples, NH₄ and NO₃ were extracted using 1 M KCl and analyzed colorimetrically (Dossa et al., 2013). For 2015 samples, a 2 M KCl extraction was performed (Maynard and Kalra, 1993), followed by automated colorimetry (USEPA, 1993a, USEPA, 1993b).

2.3.6.3. Plant nutrients

Ground plant tissue samples were prepared for elemental analysis by conducting an acid digestion (Havlin and Soltanpour, 1980). Shrub and millet leaves and stems were digested and analyzed separately but fractions were summed to calculate total nutrient
uptake. Instrumental analysis for P, K, Ca, Mg, S, Mn, Fe, Zn, and Cu was conducted by ICP-OES 700 (Agilent Technologies, Santa Clara, CA) according to USEPA method 6010C (USEPA 2007) in order to determine how much nutrients were returned to the soil in the plant biomass. Certified reference material (NIST 1573a) was used for evaluating method recovery of all nutrients. Average (10 reps) recovery was within 15% of the certified value for every element. Analysis of total N in plant material was performed on an Elemental Analyzer 1108 (Carlo Erba Instruments, Milano, Italy).

2.3.7. Statistical analysis

Data were checked for normality and homogeneity of variance assumptions. The PROC MIXED procedure in SAS (Version 9.4; SAS Institute, Cary, NC) was used for statistical analysis of the split-plot design data with year, presence or absence of shrubs, and fertilizer rate analyzed as fixed effects and blocks as a random effect. Yield, crop biomass, soil nutrients and C fractions were treated as repeated measures in time. Differences were considered significant at $P \leq 0.05$, and Tukey’s honest significant difference test was used to separate significant effects by fertilizer treatment within each year. Fertilizer effect on *P. reticulatum* biomass and nutrient uptake was analyzed only in shrub plots with a one-way ANOVA as a randomized complete-block-design. Regression analysis was used to evaluate relationships between shrub biomass and carbon fractions with millet and groundnut yield, and also to examine rainfall with shrub biomass.

2.4. Results

2.4.1. Crop yield
2.4.1.1. Millet

Between 2011 and 2015, millet grain yield averaged across fertilizer treatments ranged from 1606 to 1248 kg ha\(^{-1}\) in the +shrub plots (\(P < 0.001\)) compared to between 1236 and 894 kg ha\(^{-1}\) in the −shrub plots (Table 2.1). A significant interaction between the effect of year*shrub (\(P = 0.05\)) highlighted the different yield trends in the different plots. Namely, without shrubs, there was a 28% stepwise yield decrease for 2011, 2013, and 2015 with 1236, 1016, and 894 kg ha\(^{-1}\) respectively, whereas with shrubs, there was a decrease in millet yields between 2011 and 2013 (1606 to 1248 kg ha\(^{-1}\)) followed by an increase to 1344 kg ha\(^{-1}\) in 2015.

The shrubs significantly increased yields over no-shrub treatments from 2011 to 2015 (\(P = 0.0023\)). This contrasted with the results in Dossa et al. (2013) where the shrub effect did not significantly affect millet yields in 2005 and 2007. From 2011 to 2015, yields were 34% greater in +shrub plots over −shrub plots (averaged across fertilizer treatments) and 105% greater in +shrub plots without fertilizer. From 2005 to 2007, the respective differences were only 15 and 14% greater in the +shrub plots (Dossa et al., 2013). At \(P \leq 0.05\), the post hoc analysis showed that without fertilizer addition, yield was significantly greater in the +shrub plots during 2013 and at every fertilizer level in 2015. However, at \(P < 0.1\) the shrub effect was significant with 0 and 0.5X fertilizer treatment in 2011 as well (Table 2.1).

The effect of fertilizer on yield was very significant (\(P < 0.0001\)) and regression analysis showed that it was best fitted to a linear model (Fig. 2.2) in both the +shrub and −shrub plots (\(R^2 = 0.73\) and 0.83 respectively). There was no significant shrub*fertilizer rate interaction (\(P = 0.41\)), and the difference between the linear equations describing
fertilizer and yield relationships in the + shrub and − shrub plots (Fig. 2.2) showed that on average there was 343 kg ha\(^{-1}\) more yield with \textit{P. reticulatum} at every fertilizer level.

From the start of the experiment in 2005 to the end in 2015, WUE in the + shrub plots increased at the 0.5, 1, and 1.5X fertilizer rates by 26\%, 37\%, and 65\% respectively and decreased slightly (5\%) with no fertilizer (Fig. 2.3). In the − shrub plots, the trends were different with decreases of 38\% and 6\% at the 0 and 0.5X fertilizer rates respectively, a 5\% increase at 1X, and no increase at 1.5X. Averaged across fertilizer treatments, \textit{P. reticulatum} increased WUE by 36\%, whereas there was a 4\% WUE decrease in the − shrub plots.

\textit{2.4.1.2. Groundnut}

Groundnut yields varied by year (\(P<0.0001\)) where rainfall was 964 mm in 2012 and 513 mm in 2014. In the + shrub plots, the yields averaged across fertilizer treatments were 1727 and 1382 kg ha\(^{-1}\) in 2012 and 2014 respectively and 1687 and 1143 kg ha\(^{-1}\) in the − shrub plots (Table 2.1). Though yields were greater in the + shrub plots at the 0 and 1.5X fertilizer rates during 2012, the shrub effect was not significant. However, shrubs did increase yields in 2014 (\(P=0.0003\)) and the post hoc analysis showed that this effect was significant at the 0X fertilizer rate (Table 2.1). The yield averaged across fertilizer treatments was 2 and 21\% greater in the + shrub plots in 2012 and 2014 respectively, but 23 and 39\% greater at the 0X fertilizer rate.

WUE averaged across fertilizer treatments in the + shrub plots increased by 75, 42, 30, and 27\% at the 0, 0.5, 1, 1.5X fertilizer rates respectively from 2006 (2004 is not considered because a drought that year caused the crop to be reseeded [Dossa et al.,
to the last groundnut year in 2014 (Fig. 2.3). However, in the − shrub plots there was a 17 and 7% increase at the 0 and 0.5X fertilizer rates and a 12 and 17% decrease at the 1 and 1.5X fertilizer rates. Averaged across all fertilizer treatments, WUE increased in the + shrub plots by 43%, but decreased in the − shrub plots by 3%. Fertilizer rate did not have a significant effect on groundnut yields ($P = 0.31$)(Fig. 2.2), and in 2014, the yield in the + shrub, 0X fertilizer plot was greater than yields from plots receiving fertilizer.

2.4.2. *Piliostigma reticulatum* biomass and nutrient uptake

*P. reticulatum* aboveground biomass yields were extremely variable during the 5 years of this study ranging from 1212 to 8187 kg ha$^{-1}$ averaged across fertilizer treatments (Fig. 2.4). Averaged across all fertilizer treatments and the years 2011 to 2015, the aboveground shrub biomass addition was 3.9 Mg ha$^{-1}$ yr$^{-1}$, and in the plots without fertilizer the addition was 4.2 Mg ha$^{-1}$. Regression analysis showed a strong positive relationship between shrub biomass from the first coppice and the biomass that grew during the growing season (Fig. 2.5). There was also a positive relationship between rainfall that fell in September and October of the preceding year and biomass from the first coppicing event of the following year ($R^2=0.46$), in addition to total biomass from the following year ($R^2=0.41$)(Fig. 2.5). Interestingly, the positive relationship between same-year rainfall and shrub biomass was only nearly significant ($R^2=0.39$)(data not shown). There was also a linear relationship between total shrub biomass from 2012 and 2014 and millet yields in 2013 and 2015 (Fig. 2.6). However, there was no relationship between same-year shrub biomass production and millet or groundnut yields (data not shown). Fertilizer did not significantly affect shrub biomass
yields at either sampling or the yearly total, although fertilizer was nearly significant at the first coppice \( (P=0.11) \). In 2015, \( P. \text{reticulatum} \) aboveground shrub biomass (4.6 Mg ha\(^{-1}\) averaged across all fertilizer treatments) that was incorporated into the soil added 1395 kg C, 35 kg N, 22 kg K, 61 kg Ca, 14 kg Mg, and <3 kg ha\(^{-1}\) of the rest of the measured nutrients (Fig. 2.7).

2.4.3. *Crop biomass and millet nutrient uptake*

Shrubs significantly increased groundnut biomass in 2014 at the 0, 1, and 1.5X fertilizer rates and millet biomass in 2015 at the 1 and 1.5X fertilizer rates (Table 2.2). The overall model showed a significant shrub effect on millet \( (P=0.0051) \) and groundnut \( (P=0.017) \) and there was a consistent trend of greater crop biomass in the plots with shrubs where only one fertilizer level in 2011 and 2012 produced less biomass in the +shrub than the −shrub plots. Consistent with grain yield, fertilizer had a strong effect on millet and groundnut biomass but the interaction between shrubs*fertilizer was not significant.

In 2015, there was no significant difference between the nutrient concentration (mg kg\(^{-1}\)) in millet plants from the plots with and without shrubs. However, when the nutrient concentration was multiplied by total millet biomass at the plot level (kg ha\(^{-1}\)), the overall model showed a significant shrub effect for C, N, P, K, Mg, S, Ca, Cu, and Fe. Nevertheless, the post hoc analysis indicated that the shrub effect did not vary based on fertilizer levels except for C uptake at the 1 and 1.5X fertilizer rate (Table 2.3). Ranges for C and macronutrient uptake in millet aboveground biomass from the 0 fertilizer treatment in −shrub and +shrub plots respectively were: 455-821 kg ha\(^{-1}\) C, 15-30 kg ha\(^{-1}\)
N, 0.7-1.7 kg ha⁻¹ P, 10-17 kg ha⁻¹ K, 9-19 kg ha⁻¹ Ca, 8-16 kg ha⁻¹ Mg, and 0.9-2.3 kg ha⁻¹ S.

2.4.4. Soil carbon

The analysis of POM-C and C <53 µm showed that in the top 10 cm of soil, the smaller fraction predominated in 2012, 2013 and 2015 (Fig. 2.8). C <53 µm increased by 50% (2429 to 3645 mg kg⁻¹) in the +shrub plots from 2012 to 2015 (C <53µm and Total C were not measured from 2004 to 2007.). Notably, however, C <53µm decreased by 22% in the −shrub plots during those same years from 2332 to 1829 mg kg⁻¹. There was also a 12% increase in total C in the +shrub plots (3284 to 3682 mg kg⁻¹) but a 23% decrease in the −shrub plots (2853 to 2188 mg kg⁻¹). POM-C decreased in both plots and was only 37 and 359 mg kg⁻¹ at the end of the experiment. In addition to differences between inter-year variation in C levels from +shrub and −shrub plots, there was also intra-year variation between planting and harvest soil C levels. In 2013, +shrub C <53 µm increased from 2017 mg kg⁻¹ at planting to 2178 mg kg⁻¹ at harvest and from 2686 to 3645 mg kg⁻¹ in 2015 (data not shown). In contrast, there were decreases in the −shrub plots from 1807 to 1783 mg kg⁻¹ in 2013 and from 1912 to 1829 mg kg⁻¹ in 2015. Total C followed the same intra-year trends.

Shrubs significantly increased Total C at harvest in all three years (P=0.0018) and the post hoc analysis showed that difference was significant (P<0.04) at all fertilizer levels in 2013 and 2015 (Fig. 2.8). The shrub effect was also significant for Total C at planting in 2013 and 2015 (P<0.02). For C<53 µm, the effect of shrubs was significant at planting in all three years (P=0.0091) and at harvest sampling in 2013 and 2015 (P<0.0001). Tukey’s showed that C<53 µm was significantly greater at every fertilizer
level at harvest 2015 and at 1.5X fertilizer at planting in 2012, 2013 and harvest 2013 as well. The shrubs had no positive effect on POM-C levels in any of the three sampling years, and fertilizer rate also did not affect either of the C fractions or the total.

The analysis of soil C to a depth of 10-cm showed that at harvest there was 2534 kg ha\(^{-1}\) more C <53 µm in the +shrub plots with no fertilizer addition (5146 ± 754 SE compared to 2612 ± 354 kg ha\(^{-1}\)). For total C, the difference was 2092 kg more total C in the +shrub plots (5238 ± 718 compared to 3146 ± 186 kg ha\(^{-1}\)). At planting, the difference between +shrub and -shrub plot C <53 µm and total C was 1417 kg and 809 kg respectively. Regression analysis of carbon fractions on crop yields showed no relationship with groundnut or millet yields.

2.4.5. Soil nutrients

Of the ten essential plant nutrients analyzed in 2014 and 2015, *P. reticulatum* significantly increased the extractable levels of five of the six macronutrients (inorganic N, K, Ca, Mg, S) and two of the micronutrients (Mn and Cu) for at least one sampling period in both years. The effect of year was significant on all nutrients, and the fertilizer effect was significant on all nutrients except S and Cu. The most pronounced differences between soil nutrients from plots with and without shrubs was for Ca, K, and Mg where the post hoc analysis showed that levels were significantly greater in the +shrub plots with no fertilizer addition at all three samplings in both years (Fig. 2.9). Moreover, for those three elements the differences were significant during at least one of the sampling periods in both years at the other fertilizer levels. For inorganic N, the post hoc analysis showed that the +shrub treatment was significantly greater at 1X fertilizer for harvest 2015, for S
as well in harvest 2014, for Mn at harvest 2014 and 2015. The differences were also significant at 1.5X for Mn and Cu at harvest 2015 and at 0X fertilizer for S at harvest 2014. Across all fertilizer treatments, the levels of Ca ranged from 121 to 244 mg kg\(^{-1}\) with shrubs and from 74 to 149 mg kg\(^{-1}\) without them. For K, the respective shrub and no shrub ranges were 15 to 47 and 9 to 23 mg kg\(^{-1}\) and for Mg from 20 to 51 and 9 to 32 mg kg\(^{-1}\). Table 2.4 presents the levels of the other nutrients (inorganic N, P, Mn, Fe, S, Cu and Zn) at harvest sampling in 2014 and 2015.

2.5. Discussion

2.5.1. P. reticulatum intercropping and drought resistance

In Sub-Saharan Africa, precipitation is the most limiting factor for crop yields (Bruinsma, 2003). Moreover, the frequency, duration and consequences of droughts related to climate change are expected to increase in West Africa (Sheffield and Wood, 2008; Dai, 2013; Xue et al., 2016). Especially for the Sudanian region of the Sahel where P. reticulatum predominates, Sultan et al. (2013) predicted that 89% of the time millet yields will decrease when there is a ±20% variation in annual precipitation combined with a long-term 0 to 6°C temperature increase. Consequently, an effective conservation agriculture (CA) system must first and foremost be able to buffer crop yields against erratic rainfall.

To determine the potential of a CA system to buffer crops against drought requires long-term field studies that capture year-to-year variability in precipitation, that include dry years, and that ensure sufficient time for soils to respond to management. This study met these criteria, running from 2004 to 2015 with 9 cropping seasons and
rainfall ranging from 513 to 954 mm. The most direct evidence for the ability of *P. reticulatum* to buffer against drought is rainfall water use efficiency (WUE) values. In the +shrub plots, both millet and groundnut WUEs had a general increase over time whereas in the −shrub plots, WUEs decreased. Furthermore, the effect of shrubs on WUE was especially evident during the last three years of the experiment when precipitation was 92 to 237 mm below the regional mean annual precipitation of 750 mm (Kizito et al., 2006). Thus, optimized *P. reticulatum* intercropping systems that have high shrub densities and return coppiced biomass to the soil surface would be expected to be a significant buffer against climate change, in part because of increased WUE for millet and groundnut.

The increased WUE in +shrub compared to −shrub plots also translated to pronounced differences in true yield especially in the treatments without fertilizer during all five years from 2011 to 2015. At this site, variability kept Tukey’s test from showing more significant differences by fertilizer treatment when we set the significance level at $P \leq 0.05$ as presented in Tables 2.1 and 2.2. However, large yield variability is characteristic of the Sahel (Therond et al., 2011) where rainfall sustains crops, soils have low fertility, and external inputs are rare. Nonetheless, in this study, mean yield (averaged over fertilizer rates) differences were still significant in all millet cropping years and with groundnut in 2014. Despite the somewhat high variability of the yields, we suggest that the large percentage differences between presence and absence of shrubs are more important for assessing the yield impact of the *P. reticulatum* system than $P$ values which are a function of the data and might have been significant at $P \leq 0.05$ had one more replicate been added to each treatment.
2.5.2. *P. reticulatum* intercropping and soil quality

While precipitation is a major climatic limitation in the Sahel, organic matter input is the most limiting management factor (Bationo and Buerkert, 2001; Lahmar et al., 2012) because it controls soil organic C (SOC) which in turn impacts yields (Roose and Barthès, 2001; Bationo et al., 2007; Lal, 2010). Therefore, a beneficial CA practice must not only buffer against limited soil water but also increase SOC. The average annual addition of C from the coppiced *P. reticulatum* biomass was >1 Mg C ha\(^{-1}\) and resulted in a significant increase both in C <53 μm and total C fractions from 2012 to 2015, whereas there were decreases in the shrub plots in those same years. Thus, a millet-groundnut rotation which returned millet residue to the soil every other year but had no other organic inputs from either shrub above or belowground inputs was not able to prevent SOC losses. Similarly in Niger, there were no significant SOC increases in a 16-year continuous cropping system with similarly-textured soils (92% sand) and annual millet biomass additions of 2700 kg ha\(^{-1}\) (Adams et al., 2016). This emphasizes the importance of *P. reticulatum* in these sandy agroecosystems and a management system of coppicing, followed by spreading the residue mulch over the surface for remediating and preventing degradation of sandy soils.

In addition to SOC, enhanced nutrient availability is particularly important in the Sahel which has some of the oldest and most weathered soils in the world with low inherent fertility in the top soil (Lahmar, 2012). In this study, significantly higher levels of macronutrients in both measurement years and during all sampling periods in the shrub plots without fertilizer suggests a consistent, sustained *P. reticulatum* improvement of soil quality. These results are also consistent with reviews by Sinare and
Gordon (2015) and Bayala et al. (2014), who reported that various trees and shrubs have positive effects on soil nutrients. Negative nutrient balances (greater losses than additions to the system) are typical in the Sahel (Bationo et al., 2007). Our results, however, indicate that even if yearly millet biomass were removed from the shrub plots without fertilizer, the nutrients in the aboveground shrub biomass would still be able to provide a positive nutrient balance. Moreover, since *P. reticulatum* residues decompose quickly with up to 80% of stem and 70% of leaf tissue broken down within 8 months (Diack et al. 2000; Diedhiou-Sall et al., 2013), this is a potential mechanism for the positive linear relationship between the preceding year’s shrub biomass and the succeeding year’s millet yield. Nutrients from this organic input were mineralized and the improved soil quality contributed to higher crop yield.

### 2.5.3. *P. reticulatum* intercropping and C sequestration

Agricultural production accounts for 15-25% of global anthropogenic greenhouse gas emissions (Vermeulen et al., 2012). Nonetheless, there is a strong link between soil C sequestration and food security (Lal, 2004) which makes climate smart agricultural systems that can increase SOC especially important for food security in the Sahel (Lipper et al., 2014). Agroforestry systems have been shown to sequester C in West Africa (Bayala et al., 2007; Lufafa et al., 2008; Takimoto et al., 2008;). However, other long-term studies that practiced continuous cultivation in sandy soils of the Sahel reported that CA practices did not sequester C (Subbarao et al., 2000; Yamoah et al., 2002). Our long-term investigation confirmed that continuous *P. reticulatum* intercropping significantly sequestered C in a sandy soil over an 11-year period. First, C <53 µm was the predominant C fraction in these soils and comprised nearly 100% of the total in the
shrub plots by the end of 2015. That fraction is considered to be the protected C pool (Six et al., 2000; Kong et al., 2005). In addition, by 2015, the 2 Mg ha\(^{-1}\) more C <53 µm in the +shrub plots was merely to a depth of 10 cm suggesting that the full C sequestration potential from shrubs is much greater if SOC were measured throughout the profile explored by shrub roots. Finally, C <53 µm continued to increase from 2012 to 2015 in the +shrub plots, implying that this sandy soil had not yet reached its full C sequestration capacity. This conclusion is further supported by Aune and Lal (1997) who estimated that 1.1% SOC was the maximum limit that could be obtained in most tropical soils, which is well above the approximately 0.35% SOC levels in the +shrub plots after 11 years of shrub-intercropping.

2.5.4. Mechanisms for increased yields and WUE with P. reticulatum

Competition between woody species and crops has been widely reported in the Sahel and limits the advantage of some agroforestry systems (Bazié et al., 2012; Bayala et al., 2015). However, this was not the case for P. reticulatum. In fact, greater in-season regrowth of shrub biomass corresponded with greater millet and groundnut yields from 2011 to 2015 and also from 2004 to 2007 (Dossa et al., 2013). An important question, then, is why P. reticulatum does not compete with crops for water and nutrients and furthermore why yields and WUE are increased near shrubs. The results of this study suggest several mechanisms for this lack of competition.

First, P. reticulatum is improving soil quality and nutrient availability which could offset or overcome any competition for water and nutrients between shrubs and crops. Nutrient competition would be reduced if shrubs made more nutrients available to crops from above and belowground additions. Even if the effect of woody vegetation on
soil fertility is merely a redistribution of nutrients rather than a true gain to the system as discussed in Bayala et al. (2015), these data nonetheless showed that a *P. reticulatum* intercropping system could prevent losses of nutrients which occurred in the shrub plots without shrub inputs. The higher SOC in the shrub plots no doubt also improves soil structure and consequently root growth and nutrient uptake by the crop. This effect is consistent with other studies showing that improved soil quality increased yields in the West African Sahel (Sanou et al., 2010; Bargués et al., 2014; Bayala et al., 2015).

Several mechanisms can be attributed to limited competition for water between *P. reticulatum* and crops. One set of mechanisms is related to improved retention and availability of water from a soils perspective with the presence of *P. reticulatum*. The improvement in soil structure from higher SOC in the shrub plots increases water infiltration and storage, thus making more water available to the whole system. Moreover, the return of shrub biomass to the soil surface reduces evaporation, conserves water, and improves yield (Trail et al., 2016). The improvement in WUE especially during years with below-average rainfall was partially attributable to hydraulic lift (HL) which Kizito et al. (2012) did establish for *P. reticulatum*. HL is the movement of water from wet subsoil to drier surface soil by roots at night when photosynthesis stops and can improve the growth of plants next to the HL donor in water-limiting environments (Sun et al., 2014; Pang et al., 2016).

Another factor is the difference in spatial water use between *P. reticulatum* and crops. Kizito et al. (2007), through water balance studies, showed that millet used water at the surface whereas shrubs remove water from deeper in the profile during the rainy season. Here we suggest another mechanism that explains lack of competition between
*P. reticulatum* and crops—a temporal offset in the times when shrubs and crops take up water which is based on three lines of evidence: 1) the strong positive correlation between shrub biomass from the 1st coppicing event and shrub biomass produced during the growing season; 2) the relationship between rainfall from the end of the preceding year and the succeeding year’s shrub biomass—meaning that shrubs are getting water for subsequent growth at a time (late season) when crop water requirements are decreasing; and 3) no relationship between in-season shrub biomass production and millet or groundnut yields.

While the relationship between biomass from the 1st coppice and biomass during the growing season could be due to decomposition and release of nutrients from the 1st coppice, the lack of relationship between in-season shrub biomass and crop yield suggests that increased nutrients were not the main cause of the relationship. Moreover, the shrubs did not significantly respond to the fertilizer treatments which is further evidence that fertility was not the main cause of differences. Root turnover and nutrient mineralization deeper in the soil profile were not examined and could have contributed to inter-year differences in shrub biomass and lack of competition between shrubs and crops. Also, shrub biomass did track yearly rainfall, but the relationship between yearly rainfall and within-season biomass production was not as strong as the relationship between late season rainfall from the previous year and shrub biomass from the following year. Thus, there is strong evidence that the crops are largely using water during the early to mid-growing seasons, whereas the shrubs are using water from the late rainy season when crops are decreasing their demand for water—a remarkable ecological mechanism of two species having off-setting temporal use of rainfall.
2.5.5. Management considerations for farmers and future research of *P. reticulatum* intercropping

Although this study showed a dramatic effect of elevated *P. reticulatum* density on soils and crop productivity, it is unknown whether the optimal density is greater or less than 1000 shrubs ha\(^{-1}\). In the Nioro-du-Rip region where this research was conducted, Lufafa et al. (2008) reported 134 to 288 *P. reticulatum* shrubs ha\(^{-1}\) which means our study had densities 3 to 4 times higher than what is currently found across cropped fields. In this experiment, one shrub occupied 10 m\(^2\), and much of the positive influence of shrubs is attributable both to the shrub residue mulch spread across the surface and to belowground root turnover. Importantly, this study showed that the *P. reticulatum* intercropping system at 1000 shrubs ha\(^{-1}\) could improve yields and soil quality at the field scale and not just directly beneath the shrub canopy (Bayala et al., 2015). Frequently there is high variability of soil nutrients at a very localized scale across the Sahel (Manlay et al., 2002; Voortman et al., 2004), and more studies are needed to determine the density where shrubs can still improve yields at the field scale but not be outweighed by shrub-crop competition.

Another consideration in developing scaling campaigns for adoption of optimized shrub intercropping systems is the amount of time needed to incur measurable benefits. The shrub effect on yield was not significant in 2005 and 2007 (Dossa et al., 2013) but was significant from 2011-2015 which showed that it took >4 years to obtain consistently elevated yields when shifting to an optimized *P. reticulatum* system. Thus, the time and labor investment to establish this intercropping system might not see a return in yield increase over the short term. Importantly, however, farmers in Burkina Faso recognize
the importance of *P. reticulatum* not only for soil fertility improvement but also its economic value for construction, animal forage, and medicinal uses (Zoundi et al., 1996; Yelemou et al., 2007, 2009, 2013, 2015). These ecosystem services, therefore, are an important component of a successful agroforestry system (Sinare and Gordon, 2015), and a farmer who relies heavily on livestock production might value the significant increased groundnut biomass for animal feed from shrub-based intercropping. More participatory studies are needed to determine economic tradeoffs and overall farmer attitudes to wide-scale adoption of a high-density *P. reticulatum* intercropping system that coppices and returns biomass to the soils rather than the current practice of low shrub density and burning parts of all of the coppiced shrub biomass (Lahmar et al., 2012; Dossa et al., 2013).

Parkland agroforestry systems of the Sahel are typically composed of multiple tree species in farmers’ fields (Bayala et al., 2015). Kizito et al. (2006) and Dossa et al. (2013) mention eight other woody species scattered throughout interspaces between *P. reticulatum* in the fields adjacent to this research station. There is potentially a synergistic effect of trees and shrubs, but this is entirely uninvestigated. Future experiments, therefore, should study the effect of mixtures of woody species—for example *P. reticulatum* with *Combretum glutinosum* and *F. albida*—on crop yields to determine whether a mixed tree and shrub system might have the same results as a homogeneous shrub stand. The final challenge for *P. reticulatum* implementation is related to climate variability. Reports of the overall re-greening of the Sahel (Kaptué et al., 2015) conflict with other reports indicating declines in both alpha and beta diversity of woody species across the Sahel (Gonzalez et al., 2012; Brandt et al., 2017). This
suggests that climate effects on woody vegetation are extremely localized, and that rainfall affects the distribution of *P. reticulatum* (Yelemou et al., 2015). More studies are needed that examine the morphology and physiology of shrub and crop interactions and specifically intra-season variation due to rainfall. These studies should also examine the *P. reticulatum* intercropping system not only in Senegal but also in the other countries of the West African Sahel to determine the range of this species.

2.6. **Conclusions**

The simplicity, elegance, and potential of *P. reticulatum* to meet the current challenges of food insecurity, climate change, and land degradation is clearly evident from the results of this long-term study. First and foremost, the shrubs consistently increased groundnut and millet yields over plots without them between 2011 and 2015 indicating that the shrub intercropping system would increase food security both in adequate rainfall years and during drought periods. Furthermore, with respect to groundnut cultivation when shrubs were present, there was little further yield benefit from fertilizer addition which is an advantage for subsistence farmers who have limited resources to purchase this input.

The mechanisms behind the yield advantage were increased soil quality and WUE dynamics. Moreover, the *P. reticulatum* intercropping system is also important because it provides significant ecosystem services. First, it can simultaneously increase yield and C sequestration which is an advantage rarely seen in sandy soil agroecosystems. Thus, increasing the plant density of *P. reticulatum* along with non-thermal management of coppiced biomass in farmers’ fields would be an effective, long term strategy to capture
CO₂ emissions and store them in soil. It also increased biomass yields which are important for livestock forage.

Questions still remain about optimal shrub densities and interactions with tree species for further yield improvement. However, the outcomes of this study combined with supporting reports on specific components of the *P. reticulatum* intercropping system (Wezel, 2000; Diack et al., 2000; Kizito et al., 2006, 2007, 2012; Lufafa et al., 2008; Dossa et al., 2008; Diedhiou-Sall et al., 2013; Yelemou et al., 2009, 2013; Diakhaté et al., 2016) provide a solid foundation to launch farmer participatory projects to pilot test and demonstrate this optimized *P. reticulatum* system throughout the Sahel. The advantages of *P. reticulatum* are that the shrub is a local resource that is dominant across the Sahel, requires very little maintenance, and has multiple uses: medicinal, animal husbandry, and construction. The combined beneficial uses make this shrub-intercropping system an implementable solution for improving the livelihoods of subsistence farmers and increasing C storage to buffer against the threat of climate change.

2.7. References


Table 2.1. Effect of the presence or absence of *P. reticulatum* and fertilizer rate on crop yields over five growing seasons at the long-term research station in Nioro, Senegal.

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*P* values using Tukey's test*

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*Tukey's test was used to separate differences between pairs of `shrub and `-shrub values within the same fertilizer rate and year.*
Table 2.2. Aboveground crop biomass in the presence or absence of *P. reticulatum* under varying fertilizer rates over five growing seasons at Nioro, Senegal.

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P values using Tukey’s test*

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*Tukey’s test was used to separate differences between pairs of *+shrub* and *-shrub* values within the same fertilizer rate and year.
Table 2.3. Levels of macro-nutrients and C taken up into millet tissue (stems and leaves) at the field level (per hectare) in the presence or absence of *P. reticulatum* under varying fertilizer rates for the 2015 growing season.

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<th>K (<em>Shr</em>)</th>
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<td>1674†</td>
<td>1165§</td>
</tr>
<tr>
<td>1.5X</td>
<td>82†</td>
<td>57†</td>
<td>5.9‡</td>
<td>3.6‡</td>
<td>40†</td>
<td>28†</td>
<td>42†</td>
<td>37†</td>
<td>34†</td>
<td>21†</td>
<td>5†</td>
<td>3.9†</td>
<td>2054†</td>
<td>1471§</td>
</tr>
<tr>
<td>Mean</td>
<td>50†</td>
<td>36†</td>
<td>3.1‡</td>
<td>2.2b</td>
<td>25†</td>
<td>19b</td>
<td>30†</td>
<td>24b</td>
<td>25†</td>
<td>15b</td>
<td>3.1†</td>
<td>2.4b</td>
<td>1,459†</td>
<td>997§</td>
</tr>
</tbody>
</table>

‡Pairs of "*shrub and 'shrub values within a fertilizer rate and year followed by the same letter are not statistically different at *P*<0.1.
Table 2.4. Extractable soil nutrients (other than Ca, K, and Mg) in the presence or absence of *P. reticulatum* under varying fertilizer rates at harvest 2014 and 2015.

<table>
<thead>
<tr>
<th>Fertilizer rate</th>
<th>Total Inorganic N</th>
<th>P</th>
<th>S</th>
<th>Mn</th>
<th>Fe</th>
<th>Cu</th>
<th>Zn</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>mg kg⁻¹</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td>Shrub ` Shrub</td>
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<tr>
<td>2014</td>
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</tr>
<tr>
<td>0</td>
<td>33a‡ 25.5</td>
<td>11.5a 11.7a 5.1a 4.1b 66.2a 66.5a 24.8a 28.7a 0.32a 0.32a 0.68a 0.21a</td>
<td></td>
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</tr>
<tr>
<td>0.5X</td>
<td>36.4a 31a</td>
<td>16a 14.7a 4.4a 4.1a 62.8a 68.1a 27.2a 30.2a 0.31a 0.32a 0.31a 0.28a</td>
<td></td>
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</tr>
<tr>
<td>1X</td>
<td>32.9a 29.4a</td>
<td>20.8a 19.8a 4.5a 3.8a 64.9a 58.2a 29.7a 30.1a 0.32a 0.3a 0.29a 0.28a</td>
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<td></td>
</tr>
<tr>
<td>1.5X</td>
<td>34.6a 28.7a</td>
<td>31.8a 26.8a 4.7a 3.6b 63.4a 50.2a 31.7a 30.1a 0.33a 0.27a 0.42a 0.25a</td>
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<tr>
<td>Mean</td>
<td>34.2a 28.7b</td>
<td>20.0a 18.3a 4.7a 3.9b 64.3a 60.8a 28.4a 29.8a 0.32a 0.3a 0.43a 0.26a</td>
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<tr>
<td>2015</td>
<td></td>
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</tr>
<tr>
<td>0</td>
<td>29.6a 22.5a</td>
<td>6.9a 8.2a 3.8a 2.5a 46.8a 44.6a 13.3a 16.1a 0.31a 0.23b 1.3a 0.68a</td>
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<tr>
<td>0.5X</td>
<td>27.3a 22.6a</td>
<td>10a 10.5a 3.4a 3.1a 46.6a 46.6a 17.5a 18.1a 0.26a 0.24a 0.36a 0.6a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1X</td>
<td>36.1a 21.3b</td>
<td>15.2a 15.6a 4a 2.4a 50.9a 40.3a 17.9a 18.8a 0.27a 0.25a 1.7a 1a</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>1.5X</td>
<td>31.5a 25.9a</td>
<td>17.7a 22.5a 3.9a 3.7a 47.2a 31.9b 18.7a 18.8a 0.3a 0.22b 0.75a 0.66a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>31.1a 23.1b</td>
<td>12.5a 14.2a 3.8a 2.9b 47.9a 40.9b 16.9a 18.0a 0.29a 0.24b 1.0a 0.74a</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

‡Pairs of *shrub* and `shrub* values within a fertilizer rate and year followed by the same letter are not statistically different at *P*<0.05.
Figure 2.1. Distribution of monthly rainfall at Nioro, Senegal, from 2011 to 2015. Months that are not shown did not have any rainfall.
Figure 2.2. Regressions showing the relationship between total yearly fertilizer addition (kg ha$^{-1}$ N, P,K) and 2011-2015 millet yields on the left and 2012-2014 groundnut yield on the right in the $^+$shrub and $^-shrub$ plots. Bars represent SEM.
Figure 2.3. WUE millet (a) and groundnut (b) yield from 2004 to 2015 in +shrub and −shrub plots for the 4 fertilizer treatments. Data from 2004 to 2007 adapted from Dossa et al. (2013). Bars are SEM for the 5 cropping years.
Figure 2.4. *P. reticulatum* biomass yields from a) the first coppice, b) the growing season, and c) the annual total across the four fertilizer levels from 2011 to 2015. The connected circles above the years represent a) the rainfall that fell during September and October of the preceding year, and b) the rainfall that fell during the concurrent growing season. Bars represent SEM.
Figure 2.5. Regressions showing relationships between: a) shrub biomass from the first coppice and biomass during the growing season, b) rainfall from the preceding September and October and shrub biomass from the 1st coppice of the following year, and c) rainfall from the preceding Sept. and Oct. and total biomass from the following year. Bars represent standard error of the mean (SEM).
Figure 2.6. Regressions showing relationships between: a) shrub biomass during the growing season (excluding the first coppice) in 2012 and 2014 at 0X fertilizer and millet yield from the same plots in 2013 and 2015, and b) the total biomass (including first coppice) from 2012 and 2014 with millet yield from 2013 and 2015.
Figure 2.7. Carbon and macronutrients in the total aboveground shrub biomass from the four fertilizer treatments in 2015.
Figure 2.8. Total C and distribution of the POM-C, and C <53 µm fractions in +shrub and −shrub plots over 4 fertilizer rates at harvest in 2012, 2013, and 2015. Pairs of +shrub and −shrub total C values within a fertilizer rate followed by the same letter are not statistically different.
Figure 2.9. Soil extractable Ca, K, and Mg at planting, midseason, and harvest in the +shrub and −shrub plots at 0X fertilizer during the 2014 (groundnut) and 2015 (millet) cropping seasons. Asterisks represent significant differences within sampling date at \( P<0.05 \). Bars represent SEM.
Chapter 3: *Guiera senegalensis*: A Native Shrub Adapted to Increase Food Security and Agroecosystem Function in the Sahel

3.1. Abstract

The West African Sahel is at the nexus of extreme environmental, socio-economic, and food security challenges. Agroforestry systems that rely on maintaining scattered trees in farmers’ fields are suggested as a viable means to increase yields across the region. Frequently, however, competition between trees and crops as well as conflicting economic interests limit the efficacy of trees for wide-scale yield improvement. Here we show that a native semi-evergreen woody shrub, *Guiera senegalensis*, which is often the dominant component of the natural savanna vegetation in the Sahel, is critical for agroecosystem function in sandy soils. We examined the long-term effect of a high density (1500 shrubs ha⁻¹) *G. senegalensis* intercropping system with 4 levels of fertilizer (0 to 1.5 times the recommended rate) on the growth and yields of the staple crops pearl millet (*Pennisetum glaucum*) and groundnut (*Arachis hypogaea*) in very sandy soils (95%) of Senegal, West Africa and compared that to cropping without woody vegetation. In addition, we measured the biogeochemical cycling of nutrients, shrub and millet root dynamics, soil C sequestration, soil temperature and moisture. The *G. senegalensis* intercropping system consistently maintained yields through inconsistent rainfall and simultaneously increased soil quality and soil C sequestration in these marginal soils. We conclude that the increasing dominance of this shrub across the
Sahel, its ability to produce abundant biomass unpalatable to livestock, and its unique ecological adaptation to coppicing make this a keystone species critical for increasing food security and mitigating climate change in the Sahel.

3.2. Introduction

Farmers have adapted to the natural savanna ecosystem of the West African Sahel by allowing trees to remain scattered throughout their fields in a system known as parkland agroforestry (Bayala et al., 2014; Boffa, 1999). These trees typically have provisioning, regulating, supporting and cultural ecosystem services (Bayala et al., 2014; Sinare & Gordon, 2015), and farmers manage them to maximize economic benefits (Bayala et al., 2010; Faye et al., 2011; Fifanou et al., 2011; Teklehaimanot, 2004). Moreover, parkland agroforestry is a conservation agriculture (CA) practice (Bayala et al., 2012; Giller et al., 2009; Mason et al., 2015) promoted to increase food security (Garrity et al., 2010; Mbow et al., 2014) and carbon (C) sequestration (Lal, 2004; Takimoto et al., 2008; Verchot et al., 2007) for the region. However, the advantages of trees frequently do not translate into increases in crop yield (Bayala et al., 2012; Kessler, 1991; Sinare & Gordon, 2015) for several reasons: competition with crops for nutrients, water and light (Bayala et al., 2008; Bazié et al., 2012; Pouliot et al., 2012), low densities of <20 to 55 trees ha⁻¹ (Bayala et al., 2014; Gijsbers, 1994; Sinare & Gordon, 2015), slow growth (Sanchez, 1995), inability to withstand cultivation pressure and poor drought tolerance (Gijsbers, 1994; Gonzalez et al., 2012; Maranz, 2009). Furthermore, the different uses of trees—food, animal husbandry, construction, energy, medicine, and yield improvement (Assogbadjo et al., 2012; Bayala et al., 2012; Belem et al., 1996;
Breman & Kessler, 1995; Faye et al., 2010; Kristensen & Lykke, 2003; Lykke et al., 2004)—require management strategies that are often mutually exclusive.

Another ubiquitous component of the savanna ecosystem in the Sahel are native shrubs (Pullan, 1974; Tappan et al., 2004; Wezel, 2000). Their long-term potential to improve yields, increase food security, mitigate climate change, and prevent land degradation has largely been overlooked (Lufafa et al., 2008). This is partially because farmers manage shrubs by coppicing (cutting them to the ground) followed either by removing their residues from the field (Lahmar, 2012; A. Wezel, 2000) or burning them (Diack, 2000; Dossa et al., 2009; Lufafa et al., 2008) in order to facilitate plowing and seeding. In addition, fruits from shrubs are not as valuable as fruits from trees such as *Vitellaria paradoxa* (used to make shea butter) or *Parkia biglobosa* (used extensively for cooking sauces)(Teklehaimanot, 2004), and the most important animal fodder source during the dry season comes from a common tree, *Faidherbia albida* (Bartha, 1970), which is well-known for its reverse phenology and beneficial effect on crop growth (Garrity et al., 2010). Shrubs also do not provide shade for humans or livestock (Lykke et al., 2004; Pullan, 1974), and they lack the cultural significance of trees (Assogbadjo et al., 2012; Stoate & Jarju, 2008).

Nonetheless, the attributes of shrubs that make them well-suited for yield improvement counteract the drawbacks of trees. Namely, they establish faster (Hiernaux et al., 2009; Seghieri & Simier, 2002), regrow rapidly following coppicing and tillage events (Gijsbers, 1994; Seghieri et al., 2005), have high densities and wide distributions (Hänke et al., 2016; Herrmann & Tappan, 2013), are low-growing which prevents shading (Bégué et al., 1994), and produce abundant biomass which is infrequently grazed
by livestock (Lahmar, 2012; Lufafa et al., 2008). Based on these characteristics, our hypothesis was that there is greater potential for shrubs than trees to improve livelihoods and enhance ecosystem function in the Sahel. Those goals are particularly important for three reasons: 1) Land degradation endangers food security for 100 million people in the Sahel (FAO & ITPS, 2015), 90% of whom depend on agriculture and livestock harvesting for their livelihood; 2) Climate change is predicted to inordinately affect the region jeopardizing yields, (Dai, 2013; IPCC, 2012; Sultan et al., 2013) and 3) the United Nations (UN), through initiatives such as the Great Green Wall (Berrahmouni et al., 2014; FAO, 2016), are currently promoting and implementing sustainable land use practices to combat desertification and mitigate the effects of climate change in multiple countries of the Sahel. However, the scientific efficacy of many of these practices is unknown (O'Connor & Ford, 2014).

Accordingly, we established a long-term experiment near Thies, Senegal, West Africa, in 2004 to study the effects of the dominant native shrub in the Sahelian ecological zone, *Guiera senegalensis*, (Breman & Kessler, 1995; Lufafa et al., 2009; Seghieri et al., 2005), and its ability to improve crop growth and yields, soil C sequestration, and nutrient cycling at the field scale. The last point is essential for agroforestry research because frequently the beneficial effect of trees extends only to the edge of their canopy (Bayala et al., 2015) and with densities typically kept at fewer than 20 trees ha$^{-1}$ (Bayala et al., 2014) it is uncertain whether trees are really an effective or implementable CA practice for widespread adoption in the Sahel.

The density of *G. senegalensis* in the Sahelian ecological zone of central and northern Senegal averages from 240 to 310 plants ha$^{-1}$ (Kizito et al., 2006; Lufafa et al.,
It typically grows in stands (Bromley et al., 1997) with canopies 1.5 - 3 m high with multiple stems and has a distribution from Senegal/Mauritania to Sudan/Eritrea (Lahmar et al., 2012). Previous research has shown that *G. senegalensis* benefits soil moisture, rhizosphere biology and mineralization of nutrients, biogeochemical cycling, soil C, and crop yields in the short-term (Wezel, 2000; Diedhiou et al., 2009; Diedhiou-Sall et al., 2013; Dossa et al., 2008, 2009, 2012; Kizito et al., 2006, 2007, 2012; Lufafa et al., 2008; Debenport et al., 2015). Our objective was to examine the long-term ecological interactions between shrubs, crops, and soils in a *G. senegalensis* intercropping system with a non-thermal management regime that spread coppiced residue over the soil surface (Fig. 3.1). We contrasted this with cropping in soils without shrubs in order to determine not only whether *G. senegalensis* could sustain or increase yields over a 12-year period but also its effect on ecosystem function in sandy soils (95%) with very low nutrient availability and an average annual rainfall of 450 mm.

For this experiment, we established a randomized complete block design with plots that had either *G. senegalensis* at densities of 1500 plants ha\(^{-1}\) (+shrub) or plots with no *G. senegalensis* plants in them (-shrub). We grew pearl millet (*Pennisetum glaucum* (L.) R. Br.) and groundnut (*Arachis hypogaea* L.) in an annual rotation (except for the last two years of the experiment when millet was continuously cropped) and applied fertilizer at four different levels—0, 0.5, 1 and 1.5 times the recommended rate for the Sahelian zone. We measured crop growth and yields, shrub and crop biomass production, soil C and extractable nutrients, soil moisture and temperature dynamics, and shrub root growth patterns from coppiced and uncoppiced shrubs intercropped with millet. Data were collected from this site between 2004 and 2007 and published in Dossa
et al. (2012). The fields were fallowed from 2008 to 2010, and this current study covers the years from 2011 to 2016. We conclude that a *G. senegalensis* intercropping system is not only well-suited for sustaining yields and sequestering C in marginal soils of the Sahel but also that the coppicing mechanism followed by spreading residues over the soil surface causes ecological changes between the shrubs, crops, and soil that gives the *G. senegalensis* intercropping system a niche specificity ideal for a CA practice in this semi-arid environment.

3.3. Materials and Methods

3.3.1. Experimental site

This study was conducted at the long-term experimental station of Keur Matar Arame near Thies in the northern Peanut Basin of Senegal, West Africa (14°45’N, 16°51’W). The site is within the Sahelian climatic zone (Le Houerou, 1980). Air temperatures range from 20.0 to 33ºC and the mean annual precipitation of 450 mm mainly comes between July and September. Cumulative rainfall at KMA was quite variable for the duration of this experiment: 300, 560, 303, 578, 529, 568, 468, 331, 572, and 319 mm in 2004, 2005, 2006, 2007, 2011, 2012, 2013, 2014, 2015, and 2016 respectively (Fig. 3.1). The elevation is 43 m above sea level with 0-2% slopes, and the ecosystem is savanna—primarily shrubland with scattered trees (Diouf & Lambin, 2001). *G. senegalensis* is the predominant shrub throughout farmers’ fields with an average density of 240 - 310 ha⁻¹ (Kizito et al., 2006; Lufafa et al., 2008), and *Faidherbia albida* (Del.) A. Chev. is the dominant tree. Other woody species in fields adjacent to the site are: *Ziziphus mauritiana* Lam., *Combretum aculeatum* Vent., and *Balanites aegyptiaca*
(L.) Del., and the herbaceous annual vegetation between trees and shrubs is principally *Mitracarpus villosus* (SW.) DC, *Cenchrus biflorus* Roxb., *Digitaria lecardii* (Pilg.) Stapf., *Eragrostis tremula* (Hochst & Steud), *Indigofera pulchra* Willd., and *Stylosanthes fruticose* (Retz.) Alston (Dossa et al., 2010). At KMA the soil textural class in the top 10 cm is a loamy sand with <5% clay and 95% sand, loose consistency, and has a 5.5 pH (1:2 soil:water). Below 10 cm the soil has very little clay increase or horizon differentiation to a depth >1 m. The soil is classified as a Rubric Arenosol in FAO taxonomy (Michéli et al., 2006) and as a Typic Torripsamment in USDA Soil Taxonomy (Lufafa, 2005).

3.3.2. Experimental design

In 2000, a 0.5 ha field that had been continuously cropped for at least 50 years was selected to develop the long-term experiment. *G. senegalensis* was the only woody vegetation in the field, and from 2000 to 2003, the field was fallowed. Beginning in the winter of 2003, the experiment was setup as a randomized complete block split-plot design with the presence or absence of shrubs was the main plot and fertilizer rate as the subplot with four replicates. In total, eight main plots (46 X 6 m) were established where half of them had the density of existing shrubs increased to 1,521 plants ha\(^{-1}\) (+shrub plots) which is >6 times the average density described by Kizito et al. (2006). The other half of the main plots had all shrubs manually removed from them (−shrub plots). Each main plot was further divided into 4 subplots 10 X 6 m with a 2-m gap between them and 3 m between the main plots. The shrubs in the +shrub plots were randomly but evenly distributed (9-10 plants subplot\(^{-1}\)).
Unmanaged *G. senegalensis* will grow to be a tree, and is characterized by a dimorphic root growth pattern with the majority of the root biomass found spreading through the top 0.45 m of soil and anchored by at least one thick unbranched root which go to depths >2.5 m (Kizito et al., 2006). In the *G. senegalensis* shrub plots, the first occurred in late June before crops were sown at the start of the rainy season and was followed by one to two more coppicing events during the growing season when crops were in their active growing phases. After each coppicing event, the shrub residues were cut into 5 to 10-cm pieces and spread evenly over the surface of the soil. This contrasts with the current regional management of *G. senegalensis* where parts or all of the biomass are burned post-coppice. Shrubs regrew each dry season and reached a maximum canopy size of 1.5 m tall by 2 m in diameter.

Beginning in 2003, millet (var Souna 3) was planted in all plots and fertilized with 68.5 kg N, 15 kg P, and 15 kg K ha\(^{-1}\) to allow the plots one year to equilibrate before data collection began the following year. In 2004, groundnut (var 55-437) was planted. Thereafter, this annual rotation using the same variety of millet in odd and groundnut in even years was maintained through 2007. Data from 2004 to 2007 was published in Dossa et al. (2012). Between 2007 and 2010, the site was again fallowed, but cropping recommenced in 2011 with millet (var Souna 3) in odd and groundnut (var 77-33) in even years which continued until 2015. However, in the final year of the experiment, 2016, millet was sown instead of groundnut. Crop cultivation closely followed the standard regional farmer practices. Shallow pre-planting tillage by hand was used to prepare the seedbed. During July of each year, four to six millet seeds were manually sown in rows
at a 1- by 1-m distance (10,000 mounds ha\(^{-1}\)) and subsequently thinned to 1 to 2 seedlings per hole after germination. Groundnut was planted in July or early August with plants 15 cm apart in rows 50 cm wide. Weeding was done periodically during the rainy season either by hand hoeing or using a shallow cultivator drawn by horses.

The subplot fertilizer treatments were 0, 0.5, 1.0, or 1.5 times the recommended rate for each crop developed by Senegalese Extension (Ibrahima Diedhiou personal communication). For groundnut, beginning in 2004, the recommended rate was 9 kg N, 30 kg P, and 15 kg K ha\(^{-1}\) manually applied as a 6-20-10 blend post-germination and incorporated by hand hoeing to a depth of 5 to 8 cm. For millet beginning in 2005, the recommended rate was 22.5 kg N, 15 kg P, and 15 kg K ha\(^{-1}\) applied at planting as a 15-15-15 blend and incorporated lightly by hoe followed by a sidedressing of 46 kg N ha\(^{-1}\) as urea in 23 kg increments broadcast at 2 and 4 weeks post-planting. During all subsequent cropping years, these fertilizer treatments were maintained.

3.3.3. Crop yield assessment, WUE, and plant sampling

Yield and biomass for both crops were measured at harvest from the inner two-thirds of each subplot. For groundnut, the entire plant was mechanically dug up, sun-dried for 4 to 5 d, before the pods were separated from biomass and each fraction was weighed separately. According to common farmer practice in the region, groundnut biomass was used as fodder for livestock and not returned to the field. In 2011 during grain-filling stage, birds destroyed the entire grain crop and millet yield was not achieved. In 2013, a severe beetle attack ruined most of the grain yield and the rest was eaten by birds. When the experiment was established in 2003, the fields surrounding the site belonged to local farmers and were cropped annually in millet and groundnut.
However, after 2008, unfortunately the adjacent fields were abandoned for agricultural production because of poor soil fertility and erratic rainfall in the area, and no grain was produced within 3 km of the site from 2009 to 2016. Consequently, we suspect that the isolation of this experiment led to inordinate bird and insect pressure at grain-filling stage much more than if this site were one field among a patchwork of other crops. However, aboveground millet biomass (leaves and stalks) in 2011 and 2013 was cut at the soil surface, weighed fresh, and a subsample of approximately 500 g was used to determine the water content at 65°C. The rest of the millet biomass from each plot was then returned to the soil surface.

In 2015 and 2016, when panicle stage was reached, a select number of millet plants in each subplot had their panicles covered with cheesecloth to prevent birds and insects from eating the grain. When the grain on protected ears reached maturation and air dried to <10% water content, the panicles were harvested and the seeds were manually separated from the heads. Because the uncovered panicles were destroyed by birds, a linear relationship similar to that used by Dossa et al. (2012) was established from the unaffected millet panicles with grain on them to estimate yield from bird-affected panicles. The equation was derived from the weight of grain from an unaffected panicle along with the weight of the panicle after grain shelling:

\[ y = 0.6777x - 2.139 \quad (R^2 = 0.90) \]

where “x” is the weight of panicles without grain (because of bird damage) and “y” is the weight of grain. Estimated grain weight from panicles damaged by birds and the grain from intact, unaffected ears were summed to determine the grain weight across the plot. Millet biomass from 2015-2016 was subjected to the same treatment as biomass from
2011 and 2013 except that in 2015 a representative sample of stems and leaves from each subplot were ground with a Wiley Mill to pass a 2-mm mesh and the kept in sealed plastic bags for nutrient content analysis. Water use efficiency (WUE) values were calculated by dividing millet biomass and both crop yields by annual precipitation (kg ha\(^{-1}\) mm\(^{-1}\)) to be able to compare biomass and grain yields from 2004 to 2007 with yields from 2011 to 2016.

3.3.4. Plant growth measurements

Between 2013 and 2015, various measurements were made on millet and groundnut growth and phenology. In 2013, 15 millet plants from the 0 and 1X fertilizer treatments (5 plants from the center row of each of three subplot replications) were tagged and used to measure plant height and number of leaves at 35, 42, 52, 56, and 67 days after seeding (DAS). The percentage of the 15 tagged plants per treatment that reached panicle stage (had at least one panicle on them) was measured at 48, 52, 56, 67 and 74 DAS. Likewise, the percentage of plants in blooming stage was recorded the same way when flowers first appeared at 52, 56, 67 and 74 DAS. In 2014, 15 plants also from the 0 and 1X fertilizer subplots were used to measure groundnut height and number of leaves at 19, 26, 33, 40, 47, 54, and 61 DAS. For 2015, plant height was measured on all fertilizer treatments (0, 0.5, 1, and 1.5X) and using 15 plants/treatment at 21, 28, 35, 42, 49, 56, and 63 DAS. Number of leaves in 2015 was measured on the same dates except that counting began on 28 DAS and concluded at 70 DAS. Percentage of plants at panicle stage was measured at 52, 56, 62, 68, 74, and 78 DAS and percentage at blooming stage on 58, 64, 68, 74, 81, and 88 DAS.
We selected plant height as a proxy for millet growth rate and used the first derivative to determine both what the maximum growth rate (MGR) was and the approximate day when it occurred in 2013 and 2015. Specifically, the first derivative was used for plant height measurements on all treatment replicates between sampling dates (for example between days 35 and 42 and 42 and 52) and then the average of the rates were plotted. We only sampled every 5 to 10 days, therefore the day that the MGR apex occurred for the mean of the treatments was an approximate date.

3.3.5. Soil moisture and temperature monitoring

Soil moisture and temperature were monitored with capacitance sensors (5TM, Decagon Devices, Pullman, Washington) in the +shrub and –shrub plots receiving no fertilizer addition. In 2012, four sensors were buried carefully in the undisturbed wall of a hole at 20 cm depth in each of two +shrub and –shrub subplots near the center of the plot. Two more sensors were buried at 10 cm depth in +shrub and –shrub subplots. The moisture sensors were used with an accuracy of ±0.04 m³m⁻³ based on a gravimetric field calibration. Temperature accuracy was the factory default of ±1°C. Data was recorded in Serial mode with a multiplexer attached to a data logger (AM16/32 and CR1000 Campbell Scientific. Logan, UT). Moisture and temperature were recorded every 15 minutes and averaged by hour from May until November in the years 2013 to 2015 except when sensors malfunctioned. The mean daily volumetric water content (VWC) and max soil temperature (T) for two sensors from each treatment were measured at the 20-cm depth. Plant height in 2013 and 2014 was the average of the 5 plants from the same subplot with sensors at 10 cm. However, in 2015, height measurements were made
on plants from the three subplots without sensors at 10 cm and consequently the average of all the plant height replications was used in the plot.

3.3.6. Shrub biomass

After each coppicing event but before the residues were spread over the surface of the soil, the fresh weight of aboveground shrub biomass (separated into leaf and stem components) was recorded. A subsample of approximately 500 g of each biomass component was used for water content determination by drying the material at 65ºC until a constant weight was achieved. In 2015, representative samples of dried stems and leaves of millet and shrub were ground with a Wiley mill through a 2-mm mesh and kept in sealed plastic bags for further nutrient content analysis. Shrub biomass was analyzed as biomass from the 1st coppice, biomass during the cropping season (from the one or two rainy season coppices), and the sum of the two fractions (the total annual shrub biomass yields).

3.3.7. Shrub root growth

In the field adjoining the KMA experimental site, fine root dynamics of *G. senegalensis* were monitored during 3 successive years (2013-2015) using 9 rhizotrons (Chairungsee et al., 2013; Jourdan & Rey, 1997; Nodichao et al., 2011) installed at 0.3 m distance from the base of 6 shrubs that were >10 years old and 3 shrubs that were <3 years old when the rhizotrons were established in the winter of 2013. A pit was excavated for each rhizotron measuring 1.5 m length X 1 m width X 1.75 m depth. Each rhizotron was made of a square-shaped pane of glass (1.0 m long X 0.8 m wide and 8 mm thick) which was reinforced by a metal frame around the edge. The rhizotrons were installed on the soil profile wall facing the shrub at a 10º maximum inclination off the
vertical. After the glass pane and frame were set in place, sieved soil from the pit excavation was used to fill in the 2-3 cm gap between the soil profile wall and the rhizotron glass pane. This soil was then compacted as much as possible to restore the former bulk density and to provide good contact between glass and soil. All rhizotrons were covered by double-layer black plastic sheets to prevent light from interfering with shrub root growth. To further protect the rhizotrons from sunlight, rainfall, insects and rodents, the excavated soil pits were covered by a metal roof.

Each year, 3 shrubs >10 years old were coppiced in early July (concurrent with the first coppice in the +shrub plots) whereas the other 3 shrubs >10 years old were not. None of the young shrubs was coppiced. Millet (var Souna 3) was sown by hand 1 m X 1 m apart and 0.3-m distance from the rhizotron directly next to the shrubs. The same cultivation methods that were employed in the +shrub plots were used for the rhizotron millet.

Observation of the appearance, growth and development of shrub and millet roots started three months after the installation of the rhizotrons and was performed every week from June 17th, 2013 until November 27th, 2015. The appearance of any new roots and/or new segments of roots linked to the growth of the preexisting roots were drawn using permanent colored markers on a transparent plastic sheet affixed to each rhizotron glass pane. A different color marker was used on each sampling date. Each transparent plastic sheet filled with root drawings was digitized manually using a 91 X 124 cm format digitizer (Summagrid VI, GTCO CalComp Inc., Columbia, MD, USA) and the RhizoDigit software (CIRAD, Montpellier, France). The RhizoDigit software was used to generate and manage a database that included the date of appearance of each new root
segment, the species of plant associated with the root, the length of new root growth at each observation date, and the depth of soil where the new roots appeared.

New root growth was divided into three treatment categories: 1) coppiced shrub roots (n=3), 2) uncoppiced shrub roots (n=6), and 3) millet roots (n=9). For analysis, the total annual new root growth during the entire measurement period (2013-2015) was divided into 4, 3-month growing periods (including the 3 months when millet are primarily growing in the Sahel). The roots were further sub-divided by depth into 4, 20-cm increments from 0-80 cm and summed to give the total root production from 2013 to 2015. The percentage of new root production in time and space was recorded during the 2 ½ years of measurement.

3.3.8. Soil sampling

Soil samples for nutrient and carbon analyses were collected from 2012 to 2015 at three times during each cropping season: planting but before fertilization, approximately 60 DAS (midseason), and at harvest. A soil corer (2.5 cm diameter) was used to take 10 cores to a 10-cm depth along diagonals within the inner two-thirds of each subplot. The soil cores were then homogenized into one composite sample per subplot, air-dried, and sieved to pass through a 2-mm sieve and a 200-g subsample kept in a sealed plastic bag at room temperature before further analyses could be performed.

3.3.9. Laboratory procedures

Total soil C was determined on a C-144 Carbon Analyzer (LECO Corp. St. Joseph, MI). Particulate organic matter C (POM-C) was measured on soils from planting and harvest during 2012, 2013, and 2015 according to the methods of Cambardella and Elliott (1992). This involved placing 30-g soil samples in 100 mL of a 5 g L⁻¹ sodium
hexametaphosphate $[\text{Na}(\text{PO}_3)_6]$ solution followed by dispersion for 16 h on a reciprocal shaker. Following this step, the soil solution was passed through a 53 µm sieve, rinsed, and the fraction passing through the sieve was dried until constant weight was achieved. The total C content of the samples was then measured by combustion on the C-144 Analyzer. The difference between the C content of the slurry that passed through the 53 µm sieve and that of a duplicate undispersed soil was the POM-C $>53$ µm, whereas the C fraction of the dried slurry multiplied by the weight of the dried slurry was the C fraction $<53$ µm, and the sum of both fractions corresponded to the total soil C content. Bulk densities of 1.61 and 1.62 g cm$^{-3}$ in the $+$shrub and $-$shrub plots without fertilizer respectively (Bogie, personal communication) were used to calculate the weight of each C fraction ($>$ and $<53$ µm and total C) per hectare to a depth of 10 cm.

The macronutrients: phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sulfur (S); and micronutrients: manganese (Mn), iron (Fe), zinc (Zn), and copper (Cu) were extracted from 2014 and 2015 soil samples using a Mehlich 3 solution (ammonium-fluoride-EDTA) (Mehlich, 1984), followed by analysis on an ICP-OES 700 (Agilent Technologies, Santa Clara, CA) (USEPA, 2007). Total inorganic nitrogen (N) in the form of ammonium (NH$_4$) and nitrate (NO$_3$) was extracted using a 1 M KCl solution on 2012 to 2014 soil samples and a 2 M KCl solution on 2015 samples (Maynard & Kalra, 1993). The extracts were then analyzed colorimetrically.

An acid digestion was performed on ground plant tissue samples (millet and shrubs) from 2015 to prepare them for elemental analysis (Havlin & Soltanpour, 1980). Instrumental analysis for P, K, Ca, Mg, S, Mn, Fe, Zn, and Cu was conducted using an ICP-OES 700 (Agilent Technologies, Santa Clara, CA) according to USEPA method
6010C (USEPA, 2007) to determine how much nutrients were returned to the soil in the plant biomass. Certified reference material (NIST 1573a) was used to evaluate the method recovery of all nutrients. The average (10 reps) recovery was within 15% of the certified value for every element. Analysis of total N in shrub and millet biomass was conducted on an Elemental Analyzer 1108 (Carlo Erba Instruments, Milano, Italy).

3.3.10. Statistical analysis

Statistical analyses were performed in SAS (Version 9.4; SAS Institute, Cary, NC) and R (Version 3.3.2). The PROC MIXED subroutine was used to analyze the split-plot design data. Year, presence or absence of shrubs, and fertilizer rate were analyzed as fixed effects and blocks as a random effect. We treated yield, biomass, soil nutrients and C fractions as repeated measures in time, and significant differences were determined at \( P \leq 0.05 \). Tukey’s honest significant difference test was applied to determine significance by fertilizer treatment within each year. A two-way ANOVA was used to analyze plant growth parameters at each measurement date. A one-way ANOVA was used to examine the fertilizer effect on \( G. \ senegalensis \) biomass and nutrient uptake in the +shrub plots as a randomized complete-block-design. We determined significance between soil VWC and T in the presence or absence of shrubs using Welch’s two-sample t-test at each soil depth and by each individual year from 2013 to 2015. Finally, regression analysis was used to evaluate relationships with shrub biomass and carbon fractions as independent variables and millet and groundnut yield as dependent variables, and also to examine rainfall dynamics with shrub biomass.

3.4. Results
3.4.1. Crop yield

The impact of a *G. senegalensis* intercropping system on both millet and groundnut yields compared to cropping in bare soil was immediate, consistent and sustained. In eight seasons from 2004 to 2016, the presence of shrubs significantly increased yields. Without fertilizer addition in this sandy agroecosystem, the difference between +shrub and −shrub plots was unequivocal: millet yields were impossible to achieve in the absence of shrubs with a maximum of 21 kg ha\(^{-1}\) in 2016 (Table 3.1). Yet with shrubs but no fertilizer in those same years, yields were small but dependable (197-321 kg ha\(^{-1}\)) and furthermore increased by 48% from the first year of cropping in 2005 with 560 mm annual rainfall to 2016 with only 318 mm annual rainfall.

Millet in both +shrub and −shrub plots responded positively to fertilizer in a linear fashion which is typical for sandy soils of the Sahel (Suzuki et al., 2016). The difference between linear equations describing fertilizer and yield relationships in the +shrub and −shrub plots showed that on average there was 304 kg ha\(^{-1}\) more yield with *G. senegalensis* at every fertilizer level. Across all fertilizer treatments (0.5X-1.5X), yields were 126% greater with shrubs and because there were no yields in the −shrub plots without fertilizer, yields were 2600% greater with shrubs but no fertilizer. Tukey’s showed that +shrub and −shrub differences by fertilizer treatment were uniform in the last three millet cropping seasons and only in 2016 at the 1X fertilizer rate was the difference not significant (*P*=0.12)(Table 3.1). Complementing, the improved yields in +shrub plots was the increase in water use efficiency (WUE)—yield divided by rainfall. WUE averaged across fertilizer treatments in the +shrub plots increased by 177% but only by
76% in the shrub plots (Fig. 3.2), and in 2016 without fertilizer, there was 1.01 kg ha\(^{-1}\) mm\(^{-1}\) with shrubs but only 0.06 kg ha\(^{-1}\) mm\(^{-1}\) without them.

More than one third of cropping land in Senegal is allocated to groundnut (FAO, 2015), which is an important cash crop and consequently one that farmers typically fertilize to safeguard and maximize yields. Here we show that this might be a misplaced perception over the long-term because fertilizer application did not affect yields in 2012 and 2014 (\(P = 0.65\)). Moreover, intercropping with shrubs but no fertilizer produced yields greater than those in the shrub plots that received 1.5 times the recommended fertilizer rate in both 2012 and 2014 (Table 3.1), and in the latter year the shrub plot, 0 fertilizer yield was the highest of all treatments. In summary, yield improvement due solely to shrubs without fertilizer over plots without either of them was 133 and 145% in 2012 and 2014 respectively (\(P < 0.02\)). Averaging across all fertilizer treatments, there were 102 and 114% greater yields with shrubs.

Groundnut WUE averaged across fertilizer treatments increased by 407% between 2004 and 2014 in the shrub plots but only by 280% in the shrub plots (Fig. 3.2). There was an ~400% increase in both shrub and shrub plot WUE without fertilizer. However, the five-fold increase in WUE still translated to almost two and a half times greater yield per millimeter of rainfall with shrubs at the end of 2014 (3.07 compared to 1.25 kg ha\(^{-1}\) mm\(^{-1}\)).

3.4.2. Crop growth and biomass dynamics

Several metrics showed that intercropping with \(G.\ senegalensis\) enhanced the rate of growth and time to maturity for millet and groundnut plants (Fig. 3.3) which is an advantage for the Sahel where erratic rainfall and routine droughts can preclude harvests.
There were significantly greater numbers of leaves on millet plants in the shrub plots as early as 28 and 35 days after seeding (DAS) in 2015 and 2013 respectively (the first dates when measurements were taken). Thereafter, the significantly greater numbers of leaves continued until harvest. For groundnut in 2014, the positive shrub effect on number of leaves was evident as early as 19 DAS (Fig. 3.4). Intercropping with *G. senegalensis* similarly increased plant height beginning at 35, 26, and 21 DAS for 2013, 2014, and 2015 respectively.

We used the first derivative to determine the maximum growth rate (MGR) for millet height which occurred at approximately 45-47 days after seeding (DAS) in 2013 and 2015. In the 2013 plots with shrubs that received either no fertilizer or fertilizer at the recommended rate, MGR was 3.7 and 6.4 cm day$^{-1}$ respectively (Fig. 3.5). Whereas, in the plots without shrubs, MGR could not be determined for millet without fertilizer within the measurement period (35-67 DAS) and at the 1X recommended fertilizer rate, MGR was 3.2 cm day$^{-1}$ at ~57 DAS. In 2015, height was measured for all fertilizer levels (Fig. 3.5), and at 45 DAS, MGR in the shrub plots was 9.6, 9.0, and 12.4 cm day$^{-1}$ at 0.5, 1 and 1.5X the recommended fertilizer but did not occur within the 63 DAS measurement period for the other treatments.

By 57 DAS in 2013, 82% of millet plants in shrub plots receiving the recommended fertilizer rate had reached panicle stage, whereas it took 76 DAS for 80% of plants to reach the same stage with the recommended fertilizer application and no shrubs. In the absence of fertilizer or shrubs only 12% of plants had panicles at the end of the experiment but 83% of plants had them in the shrub plots without fertilizer. In 2015, at 68 DAS, ≥80% of millet plants receiving either 0.5, 1, or 1.5X the recommended
fertilizer had reached panicle and blooming stage in the +shrub plots, whereas only 73% of plants at 1 and 1.5X were at that stage 80 DAS in the −shrub plots. Moreover, at 0.5X fertilizer and no shrubs, only 27% of plants had panicles and 13% were blooming at the end of the experiment and without fertilizer, no plants reached blooming or panicle stage. With shrubs but no fertilizer, panicle and blooming stage plateaued at 40% of plants 74 DAS.

In addition to differences in plant growth in +shrub and −shrub plots, there were differences in nutrient concentrations (mg nutrient kg⁻¹ plant tissue) from plants in both treatments. We found significantly higher concentrations of the following nutrients in the +shrub plots: 35% > P, 23% > Ca, 61% > Mg, 40% > Mn, 21% > Fe, 36% > Cu, and 52% > Zn (data not shown). Though the post hoc analysis did not show a significant shrub effect according to fertilizer level, nonetheless only two nutrient concentrations (N and S) were not higher in the +shrub plots at every fertilizer level (though again, this was not statistically significant). These results suggest that the enhanced growth of millet in the G. senegalensis intercropping system was due to increased rhizosphere microbial communities like arbuscular mycorrhizal fungi which enhanced the uptake of nutrients leading to vigorous millet growth.

The outcome of the enhanced crop growth dynamics in the G. senegalensis intercropping system was significantly greater biomass yields for both groundnut ($P = 0.0008$) and millet ($P = 0.0026$) at the end of each cropping season (Table 3.2). Between 2004 and 2014 groundnut biomass yields grew by 93% in −shrub plots but by 187% in the +shrub plots. In the last groundnut cropping year (with only 331 mm of rainfall) the biomass yield difference between the treatments without fertilizer was 92% greater in the
shrub plots. Furthermore, the post hoc analysis revealed that the differences between presence and absence of shrubs were significant at every fertilizer level in both 2012 and 2014 and averaged across the fertilizer treatments, groundnut biomass yields were 120% with shrubs.

The importance of millet biomass in this study was twofold: 1) Biomass from each plot was returned to the soil post-harvest; therefore, millet biomass was the only source of C added to the soil in the −shrub plots, and 2) It indicated yield potential in 2011 and 2013 when grain yields were not obtained because of bird infestation at the site. The results showed that without shrubs or fertilizer, a millet stand was almost impossible to achieve between 2011 and 2016 with a maximum biomass yield of 212 kg ha\(^{-1}\) in 2013 (Table 3.2). In contrast, the minimum biomass yield in the plots with \textit{G. senegalensis} but without fertilizer was 840 kg ha\(^{-1}\) in 2011, and across the 4 years was 1072% greater due solely to shrubs. Averaged across the three fertilizer levels, the biomass yields were 458% greater. The linear response of millet biomass to fertilizer \((P <0.0001)\) was consistent with the linear response of yield to fertilizer. Nonetheless, even with fertilizer additions from 0.5 to 1.5 times the recommended rate, biomass yields from the +shrub plots still averaged 516% greater than in the −shrub plots. Importantly, biomass WUE increased by 107% in the +shrub plots with no fertilizer between 2005 and 2016 but decreased by 56% without shrubs or fertilizer (Fig. 3.2). Averaged across the fertilizer treatments, biomass WUE increased by 82% with shrubs but only by 22% without them.

3.4.3. Soil quality – carbon

The shrub-induced improvement on crop dynamics was concurrent with enhanced soil quality evidenced by soil C and nutrient data. There were significantly greater levels
of both fractions of soil C (<53 µm and POM-C >53 µm) and the total with shrubs in all three measurement years from 2012 to 2015 at both planting and harvest. In addition, POM-C which is included in the active, rapidly-mineralized soil C fraction, rose by 39% in plots with shrubs from 2007 to 2015 (1650 to 2294 mg kg⁻¹), whereas it fell by 36% (755 to 481 mg kg⁻¹) without them. Total C, which was not measured in the period between 2004 to 2007, nevertheless also increased by 11% in +shrub plots from 2012 to 2015 but decreased by 35% in the plots without them (Fig. 3.6).

Though millet biomass in all plots was returned to the soil surface after harvest, these results indicate that this organic amendment without supplementary shrub biomass addition was not able to maintain soil C levels. The magnitude of the differences between +shrub and −shrub soil C levels increased from 2012 and 2015, and at the end of the experiment in 2015, POM-C averaged across all treatments was 377% greater in +shrub plots. Total C was 127% greater, and furthermore Tukey’s test showed that these differences were all significant at every fertilizer level.

The beneficial effect of carbon on yields in the Sahel is well-established (Bationo et al., 2007). Regression analysis showed significant linear relationships between POM-C and millet biomass as well as total C and millet biomass in the +shrub plots during 2013 and 2015 (Fig 3.7 panel A). This highlights the importance of soil C for crop growth in this sandy agroecosystem. The same beneficial POM-C to millet relationship was shown in 2005 and 2007 (Dossa et al., 2012) yet without making a differentiation between the presence or absence of shrubs. Notably in 2013 and 2015, there was no relationship between soil C and millet biomass in the −shrub plots (data not shown). Furthermore, POM-C comprised approximately 50% of the total C in the +shrub plots in
all three sampling years, yet in the shrub plots POM-C comprised only 47, 36, and 26% of the total C in 2012, 2013 and 2015 respectively (Temudo et al., 2014). This suggests that there is a threshold for POM-C in these sandy soils below which millet struggles to grow. Decreases in POM-C in the shrub plots between 2007 and 2015 potentially pushed soil C levels below this threshold. The fact that fertilizer had no significant effect on any of the soil C fractions or the total but it did on millet biomass all of which was returned to the soil surface also indicates that soil C in this system is primarily derived from shrub inputs—either above or belowground through mulched biomass, root turnover, root exudates, and rhizosphere microbial biomass.

Another interesting dynamic between the C fraction <53 µm and plant growth (both shrub and millet) was revealed from the regression analysis. Though millet responded to POM-C in the shrub plots, interestingly there was no significant relationship between C <53 µm and millet biomass, yet there was a significant relationship between C <53 µm and shrub biomass (Fig. 3.7 panel B). Thus, the C fractions potentially have different effects on soil properties which cause different responses in G. senegalensis and millet. The larger and labile POM-C fraction improves fertility and physical characteristics of the soil from rapid mineralization and aggregation (Bayer et al., 2002; Diekow et al., 2005). The C fraction < 53 µm is considered to be the protected C pool (Kong et al., 2005; Six et al., 2000) which is slowly mineralized and contributes to increased water holding capacity. In summary, this suggests that millet responds markedly to the rapid turnover and mineralization of nutrients from the labile POM-C fraction whereas the slow nutrient turnover and increased water holding capacity from the smaller C fraction benefits the slow-growing grubs (Wood et al., 2016). There
was also no significant effect of fertilizer on shrub biomass indicating that *G. senegalensis* does not respond to fertility to the same extent that millet does.

Agroforestry systems in the Sahel can increase C sequestration (Lufafa et al., 2008; Takimoto et al., 2008), and the C fraction <53 µm is the most important measure for this. The effect of year was not significant on its accumulation at the end of each season ($P = 0.25$) indicating its relative stability and importance in carbon sequestration measurements. However, there was significantly greater C<53 µm in the + shrub plots at planting and harvest during all three years. Using the bulk density to calculate sequestered carbon to a depth of 10 cm at the end of 2015, the + shrub plots had 802 kg ha$^{-1}$ greater non-labile carbon in them than the – shrub plots (2974 compared to 2172 kg ha$^{-1}$). Moreover, there was 3700 more kg ha$^{-1}$ of total C in the shrub plots than in the – shrub plots (6667 compared to 2952 kg ha$^{-1}$ total C). Without fertilizer addition, the difference was 3229 kg ha$^{-1}$ more total C.

### 3.4.4. Soil quality – nutrients

We found that *G. senegalensis* significantly increased the extractable levels of 5 of 6 macronutrients (inorganic N, K, Ca, Mg, S) and 1 of 4 analyzed micronutrients (Mn) during at least 2 of the sampling periods (planting, midseason or harvest) in both 2014 and 2015. For macronutrients in the shrub plots, this difference was: 85% > inorganic N, 51% > K, 60% > Ca, 80% > Mg, and 38% > S averaged across all fertilizer treatments and the three sampling times in 2014 and 2015. Fertilizer rate affected nutrient levels for N, Ca, K, Mg, and Mn, and Figure 3.8 shows the results from the post hoc analysis for Ca, K, and Mg which had the most consistent differences between + shrub and – shrub plots at different fertilizer levels. Interestingly, the plots receiving no fertilizer always
had the highest levels of Ca and Mg, and the trend was the same for S. Yet, there was also a difference between shrubs and fertilizer rate which showed that without shrubs, the levels of Ca, Mg, and S decreased much more quickly from no fertilizer to 1.5X the recommended rate (Fig. 3.8). This suggests that the *G. senegalensis* intercropping system is stabilizing, recycling, or replenishing nutrients in the soil and that furthermore they aren’t being lost out of the system.

Total inorganic N was also analyzed separately in NO$_3$ and NH$_4$ fractions. Both fractions were significantly higher in + shrub plots at planting, midseason, and harvest in each of the 4 years between 2012 to 2015 (Fig. 3.9). NO$_3$ comprised 75 to 83% of total inorganic N at midseason and harvest in the + shrub plots without fertilizer but only 64% of the total in plots without shrubs or fertilizer. Averaged across the three fertilizer treatments, NO$_3$ was 70 to 74% of the total with shrubs and 61-62% without. In most systems, NH$_4$ is rapidly converted to NO$_3$, but the greater levels of NO$_3$ indicate either higher mineralization rates from organic N to NO$_3$ within the shrub rooting zone driven by microbial communities or that less of the NO$_3$ was leached out of the system. The mineralization rates were most pronounced in 2015 when the + shrub 0 fertilizer plots had more than 4 times the NO$_3$ at midseason (when nitrification rates are elevated) than the – shrub 0 fertilizer plots.

### 3.4.5. Shrub and crop competition ecology

An important question is how two plants competing for limited water and nutrients in an oligotrophic environment can keep from detrimentally affecting the growth of the other. To assess this, we compared the growth patterns of new roots from (1) coppiced shrubs intercropped with millet, (2) uncoppiced shrubs intercropped with
millet, and (3) the intercropped millet. Our hypothesis was that the coppicing mechanism would fundamentally alter the temporal dynamics of new shrub root formation and would allow for more beneficial uptake of nutrients by millet grown within the canopy. The results confirmed this. Figure 3.10 shows that in the 90 days post-coppice, which was the rainy season (20 July to 20 October) when millet roots were growing, only 25% of annual new shrub root production from the coppiced treatment occurred within the top 60 cm of the soil—the depth occupied by 93% of millet roots. Conversely, 73% new shrub roots from the uncoppiced treatment grew in the top 60 cm during the period from 20 July to 20 October. Thus, the coppicing mechanism reduced active root growth for *G. senegalensis* while millet roots were in their active growth phase.

This temporal offset has important spatial consequences that specifically benefit crop growth. First, the actively re-growing roots of each plant are not physically exploring the same volume of soil at the same time indicating that within-season rainfall is more available for millet which does not have the deep root system of the shrub and consequently cannot access deep soil water. Also, the nutrient flush following mineralization from organic C in the surface of the soil during the rainy cropping season would disproportionately benefit millet which has greater active root growth in the surface layers of the soil during times of high nutrient availability.

During the initial millet growth stage (GS1) when roots have typically not advanced beyond 20 cm depth, large fluctuations in soil temperature (T) and moisture are especially detrimental to germination and root growth and can lead to rapid protein misfolding in plants (Barnabas et al., 2008; Garcia-Huidobro et al., 1982; Ong, 1983). Consequently, we examined soil T and volumetric water content (VWC) in the top 20 cm
to determine if these factors could explain a lack of competition between \textit{G. senegalensis} and crops growing within their canopy influence. Figure 3.11 shows concurrent crop growth with maximum soil T at 10 cm and VWC at 10 and 20 cm depths in the +shrub and -shrub plots without fertilizer beginning 22 days before seeding and continuing until ~65 DAS in 2013-2015. The difference between average mean daily VWC in +shrub and -shrub plots from seeding to harvest was 1.6, 0.9, and 0.8% greater in the +shrub plots from 2013-2015 respectively. Average daily maximum T during the 2013-2015 growing seasons ranged from 36.4-37.0ºC in the -shrub plots but from 31.6-34.2ºC in the +shrub plots—an average difference of 3.8ºC lower in the plots with shrubs. Except for VWC at 20 cm depth in 2014, the differences between soil T and VWC from the +shrub and -shrub plots at both 10 and 20 cm depths were all statistically significant using \textit{T} tests. Surprisingly, coppicing did not affect soil T, and there were no sharp increases in the +shrub plots in the days immediately following this event. These results, therefore, highlight that the beneficial shrub effect on soil T and VWC was not primarily a shading effect from the living shrub but rather from improved soil quality (largely SOC) and the mulch spread over the soil surface which prevented evaporation (Kizito et al., 2007; Trail et al., 2016) and decreased temperatures (Gupta et al., 1983).

Shrub biomass production varied widely by year ($P<0.0001$) ranging from 2964 to 8318 kg ha$^{-1}$ in 2014 and 2016 respectively (Fig. 3.12). However, fertilizer had no effect ($P>0.4$) on either the shrub biomass from the 1$^{st}$ coppice (i.e., the biomass that grew during the dry season), the rainy season regrowth of shrub biomass, or the annual total (the sum of the two fractions). The second panel of Figure 3.12 shows that to a limited extent shrub biomass during the cropping season tracked rainfall. However, as
was shown by Bright et al. (2017) for the shrub *Piliostigma reticulatum* in the southern Peanut Basin of Senegal, the data suggest that to a limited extent *G. senegalensis* also relies on water from the end of the previous growing season (August to October) to sustain the following year’s biomass production. The evidence for this are that there was a strong correlation between shrub biomass from the 1st coppice and in-season biomass regrowth (Fig. 3.13); there was no fertilizer effect on shrub biomass indicating that the shrubs do not respond to added nutrient additions; and there was a relationship (though weak) between rainfall from the previous August to October on shrub biomass the following year (Fig. 3.13). For extended discussion on this novel mechanism, see Chapter 2, section 2.5.4. Thus, large rainfall events with fast infiltration in these sandy soils which may not be beneficial to crop growth could nonetheless be increasing shrub biomass in the following year.

In 2015, we measured the nutrient and C uptake into leaves and stems of *G. senegalensis* biomass in 2015 and found that the annual addition to the soil surface in the shrub plots was: 1739 kg C ha⁻¹, 50 kg ha⁻¹ N, 26 kg Ca ha⁻¹, 16 kg K ha⁻¹, 11 kg Mg ha⁻¹, 4 kg S ha⁻¹, 3 kg P ha⁻¹, and <1.5 kg ha⁻¹ of the other nutrients (data not shown). Furthermore, there was a slight relationship between annual shrub biomass production and groundnut yields from the following year ($R^2=0.33$) and also on shrub biomass and millet biomass from 2 seasons later ($R^2=0.43$)(data not shown) which suggests that decomposition and mineralization of nutrients from the biomass are being taken up by the crops. The greater nutrient concentrations in 2015 millet tissue further support this interpretation.
3.5. Discussion

It is forecast that global food production must increase up to 110% by 2050 to keep pace with population growth and changing diets (Tilman et al., 2011). This challenge is compounded by climate change. Within sub-Saharan Africa, specifically, the task of developing self-sufficient food systems buffered against projected droughts and rising temperatures is even more formidable (van Ittersum et al., 2016). There are options for feeding the world without deforestation or compromising major ecosystems (Erb et al., 2016; Mauser et al., 2015), yet climate smart agricultural systems (Lipper et al., 2014) that can simultaneously increase yields and C sequestration by means of afforestation are rarely feasible or discussed. Nonetheless, these systems are critical to offset the 15-25% of global anthropogenic greenhouse gas emissions produced by agriculture (Vermeulen et al., 2012). Results from this study indicate that this potential exists with the *G. senegalensis* intercropping system in the Sahel.

First and foremost, the most-important outcome from this study for subsistence farmers is that a *G. senegalensis* intercropping system significantly improved both millet and groundnut yields over cropping without shrubs in every year which yields could be obtained from 2004 to 2016. Thus, the return on investment for implementing this system would be immediate and sustained which is critical when considering the potential for adoption of any conservation agriculture (CA) practice in the Sahel (Lahmar et al., 2012). Furthermore, the 126-2600% greater yields in the *G. senegalensis* intercropping system compared to no-shrub cropping are larger than most yield differences from CA practices—mulching, green manure, reduced tillage, mixed crop
intercropping, and agroforestry—in sub Saharan Africa (Bationo et al., 2012; Bayala et al., 2012; Giller et al., 2009; Mason et al., 2015a, 2015b).

The sustained, large differences in WUE yield between +shrub and −shrub plots indicates the ability of this system to buffer against erratic rainfall which is the most limiting factor for crop yields in the Sahel (Sarr et al., 2013). Organic matter is the most limiting management factor in the region (Lahmar et al., 2012) because of its effect on yields (Bationo et al., 2007; Lal, 2010), and this experiment showed increasing soil C with shrubs but decreasing levels in the plots without them further highlighting the suitability of this system as a CA practice. Lufafa et al. (2008) found that the average total C to a depth of 20 cm in the Keur Matar region was 1.12 Mg ha\(^{-1}\), whereas the results of this study indicate greater C levels to a depth of 10 cm in the *G. senegalensis* intercropping system. Consequently, this system has significant C sequestration potential which is strongly linked to food security (Lal, 2004) and likewise important for C trading markets.

The concurrent greater levels of available soil nutrients and nutrients in millet tissue suggest not only an improvement in soil quality but that these nutrients are not being lost from the system due to leaching or erosion. Rather the results suggest that beneficial biological communities in the shrub rooting zone (Debenport et al., 2015; Diedhiou et al., 2009; Diedhiou-Sall et al., 2013) are increasing their plant uptake. This is of fundamental importance in the Sahel which has some of the oldest and most weathered soils in the world with very low inherent fertility (Bationo et al., 1998; Lahmar et al., 2012).
The parklands of the Sahel are unique landscapes where humans have maintained the natural savanna ecosystem but in a modified state by selecting for certain woody vegetation that has perceived economic benefits (Brandt et al., 2016; Haglund et al., 2011; Maranz & Wiesman, 2003; Rasmussen et al., 2001). Overall, the Sahel has experienced a ‘regreening’ (increase in woody vegetation cover) since the droughts in the 1980s (Brandt et al., 2015; Kaptué et al., 2015). Yet, parkland vegetation is in a state of constant flux (Tappan et al., 2004), and studies indicate that the regreening has been characterized by increases in shrub rather than tree species, and furthermore that *G. senegalensis* is the principal shrub species (Brandt et al., 2017; Hänke et al., 2016; Herrmann & Tappan, 2013). The dominance of shrubs, which are typically more drought-tolerant than trees, during a time of higher rainfall and regreening suggests that human management practices and intensified land use are causing the shift in vegetation (Hänke et al., 2016; Herrmann et al., 2005; Larwanou & Saadou, 2011; Rasmussen et al., 2014).

Historically, fallowing was a principal management strategy to restore fertility in the Sahel (Wezel, 2000) where farmers would keep plots of land out of production for a period of years in order to increase fertility and allow trees to establish and regenerate. However, this technique is being abandoned with more frequency (Hiernaux et al., 2009; van Vliet et al., 2013) because of population growth and grazing pressure. Consequently, the ability of *G. senegalensis* to thrive after coppicing (Seghieri et al., 2005) and its relative unpalatability to livestock (Wezel & Bocker, 1999) makes it well-suited for these changing anthropogenic pressures. In addition to the effect of socioeconomic pressure on landscape dynamics, farmers in the Sahel also manage for climate change and shift their
management styles to meet the variability (Zorom et al., 2013). Accordingly, the recent changes in woody vegetation toward more drought-tolerant and fast-growing species in decades with higher rainfall than the 1970s and 1980s also suggests that farmers in recent decades are selecting for drought tolerant species to buffer against future climate unpredictability (Hänke et al., 2016).

*G. senegalensis* is a pioneer species (Brandt et al., 2017) that can rapidly populate areas affected by drought and low fertility degraded soils (Hänke et al., 2016; Hejcmanova-Nezerková & Hejcman, 2006; Hiernaux et al., 2009; Lahmar et al., 2012). It has drought tolerance (Gijsbers et al., 1994; Seghieri et al., 2005) and this is attributable to roots that can sustain the plant by accessing deep soil water (Gaze et al., 1998; Kizito et al., 2006). In this study, the differences in temporal and spatial shrub root production between coppiced and non-coppiced plants indicates that the coppiced shrubs are not competing with crops for water during the early rainy season when water is critical for crop establishment. The rainfall data further suggest that *G. senegalensis* is using water from the previous rainy season which further aids our understanding of why the different species are not competing for limited resources. Crops in the *G. senegalensis* plots were more robust and able to reach maturity faster than in plots with bare soil as a result of the offset in water use.

Gaze et al. (1998) noted that an ideal agroforestry species would be one with a minimal water requirement during the early rainy season, and the data from this research suggests that for *G. senegalensis* within the context of an intercropping system managed by coppicing. Furthermore, the unusually large root to shoot ratio of *G. senegalensis* (Lufafa et al., 2009) and the fact that its roots can extend up to 8 m laterally from the base
of the shrub (Gaze et al., 1998) make the species ideally suited for erosion control in sandy soils as well as nutrient cycling from root turnover. Other studies examining *G. senegalensis* and crop interactions have recorded the positive shrub effect on erosion control and sediment entrapment on crop growth (Geiger & Manu, 1993; Wezel et al., 2000). Positive relationships between shrub biomass production and succeeding year’s crop yields suggest that nutrients from this shrub mulch spread over the soil surface were mineralized and improved subsequent crop growth. The soil temperature and moisture results also signify that the mulch reduced evaporation and soil temperatures which favored crop growth (Trail et al., 2016). Because *G. senegalensis* is rarely grazed in the dry season and consequently accumulates significant biomass (Lufafa et al., 2008), there is real potential for this shrub to act as a renewable source of mulch in the Sahel.

It is unknown whether *G. senegalensis* densities <1,500 shrubs ha\(^{-1}\) would have the same effect on crop yields as what was seen in this study, and there is some evidence that lower densities with coppicing would still have an impactful yield increase (Wezel, 2000). Nonetheless, this research showed that that density was achievable and could sustain long-term crop growth at the field scale. The last two points are critical because long-term experiments in the Sahel are rare (Bationo et al., 2012), and there is a high variability in soil nutrients at an extremely localized scale (Voortman et al., 2004) which makes experiments that measure the effect of agroforestry systems on crop yield at the field scale imperative (Kuyah et al., 2016; Sinare & Gordon, 2015).

Though farmer preferences for a *G. senegalensis* intercropping system were not considered in this experiment, importantly *G. senegalensis* does have important provisioning ecosystem services—fuel, construction and medicine (Arbonnier, 2004;
Wezel & Bocker, 1999)—which increases the utility of the species for local communities. *G. senegalensis* might also be integrated synergistically with trees. The shrub does track rainfall, and Brandt et al. (2017) recorded a die-back of *G. senegalensis* species in some drier areas of Senegal. However, in that survey, the demise of established shrubs was concurrent with new shrub regeneration. This experiment also confirmed a strong relationship between *G. senegalensis* and rainfall with large variations in annual shrub biomass production. Importantly, however, the intercropping system was still able to sustain crop yields even in years with low shrub biomass production which suggests that shrub root dynamics might be more important than the shrub mulch for ecosystem function. The importance and utility of the species, therefore, might not be in its longevity but in its ability to establish and regenerate quickly especially in degraded, marginal soils where farmers struggle to achieve yields.

### 3.6. Conclusions

The results of this experiment reinforce the importance of woody vegetation for ecosystem function in the Sahel. Recent studies suggest, however, that it is shrubs rather than trees which undergird the savanna ecosystem in the central and northern Sahelian zone. We conclude, therefore, that a farming system that adapts the growth of shrubs to that of annual crops is fundamental to agroecosystem function. The *G. senegalensis* intercropping system, studied in this chapter, prevents land degradation, enhances soil quality on marginal lands, sequesters C to mitigate the detrimental effects of climate change, and improves the livelihoods of subsistence farmers.
Moreover, the *G. senegalensis* intercropping system meets the four critical criteria for implementation in the Sahel: 1) It is a free, abundant, renewable resource with a wide distribution; 2) It has more than one ecosystem service which do not mutually limit each other; 3) It buffers against drought; 4) It increases soil C and thus soil quality. Future studies should include this shrub intercropping system in participatory farmer trials.

Though trees are larger and take up more of the imagination, we suggest that shrubs, specifically *G. senegalensis*, appear to be the drivers of ecosystem function in sandy, degraded soils of the Sahel, and that the future of agroforestry in the region is with them.

3.7. References


FAO, & ITPS. (2015). *Status of the world's soil resources-main report*. Rome, Italy:


Table 3.1. Effect of the presence or absence of *G. senegalensis* and fertilizer rate on crop yields between 2012 to 2016 at the long-term research station in Keur Matar Arame, Senegal.

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<td>Shrub</td>
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<tr>
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<td>1015±139a</td>
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<td>400b</td>
<td>921a</td>
<td>429b</td>
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‡ *Pairs of* Shrub and Shrub *values within a fertilizer rate and year followed by the same letter are not statistically different using Tukey’s Test at *P*≤0.05.
Table 3.2. Crop biomass in the presence or absence of *G. senegalensis* over varying fertilizer rates from 2011 to 2016 at Keur Matar Arame, Senegal.

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<tr>
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<td>1037a 506b</td>
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<td></td>
</tr>
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<td>2306a 1280b</td>
<td>1520a 380b</td>
<td>4527a 1993a</td>
<td></td>
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‡ Pairs of *shrub and shrub values within a fertilizer rate and year followed by the same letter are not statistically different using Tukey’s Test at *P*≤0.05.
Figure 3.1. Distribution of annual rainfall by month from 2011 to 2015 corresponding with the shrub management scheme in a *G. senegalensis* intercropping system.
Figure 3.2. Water use efficiency (WUE) millet biomass (a), WUE millet yield (b) and WUE groundnut yield from 2004 to 2015 in "shrub and "shrub plots for the 4 fertilizer treatments. Data from 2004 to 2007 adapted from Dossa et al. (2012). Bars are SEM for the 6 cropping years.
Figure 3.3. A) Plant growth measurements from the plots with shrubs (turquoise) and without shrubs (red) with varying fertilizer rates. B) Photo illustrating superior growth of millet in a +shrub plot (right) compared to the −shrub plot (left) in 2016. Photo courtesy of Matthew Bright.
Figure 3.4. Number of groundnut leaves from 0-61 days after seeding (DAS) in the "shrub and ~shrub plots at the 0 and 1X fertilizer rates in 2014.
Figure 3.5. Plots showing the 1\textsuperscript{st} derivative of millet height in 2013 and 2015 in $^+$shrub (blue) and $^-$shrub plots (red) for 2013 and 2015.
Figure 3.6. Total C and distribution of the POM-C, and C <53 µm fractions in +shrub and −shrub plots over 4 fertilizer rates at harvest in 2012, 2013, and 2015. Pairs of +shrub and −shrub total C values within a fertilizer rate followed by the same letter are not statistically different.
Figure 3.7. Regressions showing relationships between: A) carbon fractions (POM, C<53µm and the total) and millet biomass from 2013 and 2015 in shrub plots, and B) C<53µm and shrub biomass fractions.
Figure 3.8. Levels of extractable soil macronutrients Ca, K, and Mg from the “shrub and” shrub plots for all four fertilizer levels at planting, midseason and harvest in 2014 and 2015.
Figure 3.9. Total soil inorganic N in 2013 – 2015 at planting, midseason and harvest in +shrub and –shrub plots. Asterisks indicate overall significance between presence and absence of G. senegalensis.
Figure 3.10. Total annual new root growth for coppiced and uncoppiced *G. senegalensis* as well as millet grown next to the coppiced shrubs from 2013 to 2015.
Figure 3.11. Crop height, soil daily max temperature, and soil moisture in the presence and absence of *G. senegalensis* without fertilizer addition. Crop height was plotted from the same blocks where sensors were in 2013 and 2014, but for 2015 the average height of millet plants was taken from the three blocks without a sensor.
Figure 3.12. *G. senegalensis* biomass at varying fertilizer rates from 2011 to 2016.
Figure 3.13. Relationships between: A) shrub biomass from the first coppice and biomass that grew during the rainy season, B) Rainfall from the end of the preceding year and shrub biomass from the 1st coppice of the subsequent season, C) Rainfall from the end of the preceding year and shrub biomass that grew during the subsequent rainy season, D) Rainfall from the end of the preceding year and the total biomass from the subsequent season.
Chapter 4: Arbuscular Mycorrhizal Fungal Ecology and Soil Nutrients in a *Guiera senegalensis*-Pearl Millet Intercropping System Across a Rainfall Gradient of Senegal

4.1. Abstract

*Guiera senegalensis*, a ubiquitous, native shrub in the West African Sahel (WAS), can improve the yields of staple crops growing within its rooting zone. However, no research has been conducted on the contribution of arbuscular mycorrhizal fungi (AMF) to the enhanced growth. Consequently, this study was the first to examine AMF ecology and soil chemical properties in the *G. senegalensis* rooting zone and in millet growing near and far from the shrub in the Sahelian and Sudanian zones of Senegal. AMF root colonization was measured in shrubs and millet plants. Soil samples adjacent to roots were analyzed for chemical properties and for AMF communities using fatty acid methyl ester (FAME) profiling. In addition, a survey was conducted to examine spore communities near and far to shrubs. Results showed high colonization rates at all sites but significantly greater colonization rates in the drier Sahelian zone. A similar pattern was observed for the AMF FAME analysis with significant differences between sites and greater abundance of FAMEs in the northern region. In total, twenty-four spore morphotypes were identified belonging to twelve genera and five families. Sixteen morphotypes were characterized to the species level including thirteen which have not been previously noted in the WAS. Soil samples near to shrubs had higher levels of C and all nutrients except for Cu and Zn, and millet growth was significantly enhanced near
shrubs. Furthermore, all nutrients were positively correlated with C indicating that the beneficial shrub effect on soil fertility is tied to increased levels of soil organic carbon (SOC). In addition, the high AMF colonization rates suggest a large mycelial network between shrubs and millet that could also increase SOC and nutrient levels from hyphal turnover. This study advances knowledge of AMF soil ecology and root dynamics in a native shrub-intercropping system of the WAS, and the results can be used to guide further mechanistic experiments.

4.2. Introduction

From Senegal to Niger, native shrubs frequently comprise the dominant woody vegetation of savanna ecosystems in the West African Sahel (WAS) (Brandt et al., 2017; Hänke et al., 2016; Herrmann & Tappan, 2013). They can be found growing throughout farmers’ fields, yet farmers typically treat them as an impediment to cultivation and manage them by coppicing (cutting down to the ground) followed by burning or removing the residues before seeding (Lahmar et al., 2012). Recent studies, however, have shown that two of the most ubiquitous shrubs, *Guiera senegalensis* and *Piliostigma reticulatum*, can increase yields and enhance the growth of the staple crops in the region (Bright et al., 2017; Dossa et al., 2012, 2013). These experiments examined the effect of shrub intercropping on soil carbon, nutrient cycling and water use efficiency (WUE). The results showed robust increases next to shrubs, and the researchers concluded that this was primarily due to improved soil quality – both chemical and physical properties – from root decomposition and incorporating shrub residues into the soil instead of burning
them. Nevertheless, the role that soil biological processes played in yield differences between crops grown near and far from shrubs was not investigated.

To date, only eight articles have investigated the soil rhizosphere biology in shrub-based agroforestry systems of the WAS. The first two studies found both a larger microbial biomass dominated by fungi and also faster leaf decomposition rates within *G. senegalensis* and *P. reticulatum* rooting zones (Diedhiou et al., 2009; Diedhiou-Sall et al., 2013). Other articles examined the nematicidal properties of *P. reticulatum* against plant parasitic nematodes (Chapuis-Lardy et al., 2015; Diakhaté et al., 2013). Hernandez et al. (2015) described an overall higher soil biological activity when mango trees (*Mangifera indica*) were intercropped with *P. reticulatum*. Similarly, Diakhaté et al. (2016) showed a more diverse and active microbial community along with higher activity of the soil enzymes urease, arylsulfatase, and dehydrogenase within the rooting zone of *P. reticulatum*. The only other work examining the soil biology within either *P. reticulatum* or *G. senegalensis* intercropping systems found a much higher diversity of rhizosphere microbial communities and specifically beneficial microorganisms in pearl millet (*Pennisetum glaucum*) intercropped with *G. senegalensis* (Debenport et al., 2015).

Arbuscular mycorrhizal fungi (AMF) research within shrub-based intercropping systems of the WAS is conspicuously absent from the literature. The AMF consist of nearly 300 species of soil microorganisms within the fungal phylum Glomeromycota (Schüßler, 2017). They form an obligate symbiosis with approximately 80% of terrestrial plants (Smith & Read, 2008). Their hyphae simultaneously colonize roots and the soil matrix where mineral nutrients are taken up and transferred to the root in exchange for plant-assimilated carbon (Smith & Smith, 2011). AMF benefit plants by improving soil
nutrient uptake (especially P) (van der Heijden et al., 2015) and by enhancing plant resistance to drought and root pathogens (Augé, 2001, 2004; de la Peña et al., 2006; Johnson & Gilbert, 2015). Furthermore, they improve soil structure which improves water holding capacity, gaseous exchange, and root growth (Rillig & Mummey, 2006). Other research has shown that a significant portion of the earth’s soil C passes through the AMF hyphal networks (Soudzilovskaia et al., 2015). Moreover, the large surface area of AMF soil mycelial networks can reduce nutrient losses after hard rainfall events by effectively acting as a nutrient interception net (Cavagnaro et al., 2015).

There is a threefold importance for a thorough understanding of AMF symbioses in shrub-based intercropping systems of the WAS. First, soils in the region are some of the oldest and most-weathered in the world with extremely low natural fertility (Bationo et al., 1998). Research has shown that there is often an inverse relationship between soil fertility and AMF abundance, and furthermore that AMF are prevalent in arid and semi-arid soils with low organic matter (Allen et al., 1995; Bradley et al., 2006; Smith & Smith, 2011). This suggests that AMF are especially important for soil function in the region. Second, farmers throughout the WAS typically use very little synthetic fertilizers or pesticides (Breman & Kessler, 1997; Vanlauwe et al., 2011), and tillage is accomplished by shallow cultivation with animal traction on small farms of 1-5 hectares. Though unintentional, this form of agriculture is a de facto organic production system, and these have been shown to maintain greater AMF diversities than conventional systems (Manoharan et al., 2017). Reducing the use of fertilizers, pesticides, and tillage can also enhance the impact of the AMF symbiosis on plant growth (Plenchette et al., 2005; Säle et al., 2015). Moreover, AMF are critical for sustainable agricultural
intensification (Rillig et al., 2016). This suggests that the socioeconomic constraints of the region require management strategies that depend on AMF. Finally, woody vegetation with deep tap roots in other arid environments can perform hydraulic lift (HL) and then transfer water to receiver plants through a common mycorrhizal network (CMN) (Querejeta et al., 2003; Egerton-Warburton et al., 2007; Prieto et al., 2011;). In the Sahel, where water often limits crop production, (Sarr et al., 2013), Kizito et al. (Kizito et al., 2012) demonstrated that *G. senegalensis* and *P. reticulatum* performed HL. This leads to a hypothesis that HL water might be transferred to crops growing within the rooting zone influence of shrubs.

The overall objective of this study, therefore, was to perform the first-ever research on AMF ecology in a *G. senegalensis*-pearl millet (*Pennisetum glaucum*) intercropping system across a precipitation gradient in Senegal. Our hypothesis was that there would be higher levels of soil nutrients and a greater AMF species richness and abundance in the rooting zone of *G. senegalensis* compared to bare soil outside of the rooting zone influence of the shrub. We further hypothesized that the higher AMF density within the shrub rooting zone would lead to higher AMF colonization rates in millet roots growing near to shrubs. Our final hypothesis was that higher colonization rates within shrub rooting zone would correlate with improved millet growth. Accordingly, we conducted a survey of millet and shrub root colonization, spores, fatty acid methyl esters (FAME), and growth dynamics in four farmers’ fields (two in each rainfall zone) across the Sahelian and Sudanian ecological zones of Senegal.

4.3. *Materials and Methods*
4.3.1. Study sites

Research was conducted along a north-south transect in Senegal to capture the two principal ecological zones of the WAS – the Sahelian zone receiving annual rainfall of 100-600 mm and the Sudanian zone with 600-1500 mm (Le Houerou, 1980). Accordingly, two sampling sites were selected for each zone that were also situated within districts used for dryland cropping within the Peanut Basin: Louga and Kaolack receiving 200-300 and 800-1200 mm precipitation yr\(^{-1}\) respectively. The Sahelian sites in Louga were Ndiaye Thioro (15º11’N, 16º35’W) and Khoyele (15º11’N, 16º01’W), and the Sudanian ones in Kaolack were Thiarene (13º50’N, 16º16’W) and Paoskoto (13º46’N, 15º48’W) – hereafter referred to as sites A and B in the north and X and Y in the south respectively (Fig. 4.1). Air temperatures at the sites ranged from 20ºC in December-January to 36ºC in April-June. Rainfall occurred in one rainy season usually in brief, scattered, but intense showers beginning in June-July and lasting until October.

The sampling sites each consisted of a field between 1-5 hectares large managed by subsistence farmers in a yearly pearl millet (\textit{Pennisetum glaucum}) and groundnut (\textit{Arachis hypogaea}) rotation (though pearl millet was frequently double-cropped). Texture-by-feel (Vos et al., 2016) was used to determine that the soils contained >80% sand in the surface horizon (0-40 cm). All fields received no inputs of synthetic fertilizer or other amendments, and seeding and weeding were accomplished either by hand or by animal-drawn shallow cultivators to a 5-cm depth. A greater density of randomly-dispersed shrubs than trees were scattered throughout farmers’ fields at each site, and overall, the Sudanian zone had more shrubs than the Sahel. However, at the northern sites, \textit{G. senegalensis} was the predominant woody species, whereas in the south it was \textit{P}. 
reticulatum. Other woody vegetation in the Sahelian zone consisted of a few species of *Faidherbia albida* (Del.) A. Chev., *Combretum aculeatum* Vent., *Ziziphus mauritiana* Lam. and *Balanites aegyptiaca* (L.). In the Sudanian zone, *Cordyla pinnata* and *Prosopis Africana* trees present in farmers’ fields. The area between shrub stands was often poorly weeded and naturally characterized by herbaceous vegetation consisting of assorted annuals dominated by *Alysicarpus ovalifolius* (Schum.) J. Leonard, *Cenchrus biflorus* Roxb., *Dactyloctenium aegyptium* (L.) Willd., *Eragrostis pilosa* (L.) P. Beauv., and *Merremia tridentate* (L.) Hall. (Dossa et al., 2010).

Farmers at all sampling sites managed shrubs by coppicing then burning the residues at the base of the shrub before seeding commenced in June-July. During this study (both cropping seasons), millet was sown in all fields at approximately 10,000 plants ha$^{-1}$. The farmers planted adjacent to the freshly-coppiced shrubs and consequently millet could be found growing <1 m from them. Shrubs re-grew at each of the sites following the May-June coppicing.

4.3.2. Experimental design

Three ecological surveys were conducted at the aforementioned sites. They occurred during the 2013 rainy season (August-October), at the end of the following dry season (June, 2014), and during the 2014 rainy season (August-September). The experimental design was a completely randomized factorial with two factors: the first was by region (either the Sahel or Sudan) and the second by sampling location to shrub. The latter treatments were determined by randomly selecting *G. senegalensis* shrubs at each site that were >10 m from any other woody species. A transect was marked off through the base of each shrub with two millet plants <1 m from the base of the shrub but 180°
apart (near millet) and two >5 m from the shrub and also 180º apart (far millet). The
2013 rainy season survey examined AMF colonization in shrub roots (n=6) and in near
and far millet (n=12). Soil samples were also taken adjacent to the roots of each plant for
chemical analyses and to examine AMF communities using fatty acid methyl ester
(FAME) analysis. The same factorial design was used for a second AMF FAME survey
during the 2014 rainy season (n=6 for all treatments). The 2014 dry season survey
examined AMF spore communities with a 2 X 2 factorial design at the same sites but
with sampling done only near or far from shrubs (n=4).

4.3.3. 2013 survey

Millet sampling was planned to coincide with panicle set (~60 days after seeding)
at each of the four sites so that all plants would be at the same physiological stage. The
rationale was that the AMF symbiosis would be at its peak during panicle set when
nutrient demands are high. Accordingly, the site visits were staggered to take advantage
of the earlier onset of the rainy season in the Sudanian zone (often 2 weeks to 1 month
prior to arrival in the Sahelian zone). However, due to a very late and uniform arrival of
the 2013 rainy season across Senegal, combined with logistical difficulties, most of the
Y-site millet plants did not have panicles.

Millet plant height was measured to the top of the tallest leaf before the entire root
system was carefully excavated with a hand spade to a depth of approximately 40 cm.
The aboveground biomass was separated from the root system by a machete and taken
back to the Institut Sénégalaise de Recherche Agricoles (ISRA) laboratory in Dakar
where fresh biomass weight was recorded. Millet root systems were placed in plastic
bags and transported by cooler to the ISRA lab in Dakar where they were stored at 4ºC.
A soil corer (2.5 cm diameter) was used to take a composite soil sample of 3 cores to a 20-cm depth adjacent to each sampled millet plant. A composite sample was also taken from the base of the shrub. Soil samples were taken back to the lab, passed through a 2-mm sieve and a subsample was used to determine gravimetric soil water content by drying at 105°C for 24 h. Another subsample was stored at -20°C until it could be processed for FAME, and the rest of the soil was air-dried and stored at room temperature for further chemical analyses.

The roots of all 6 *G. senegalensis* shrubs at each site were sampled for AMF colonization rates using the following protocol. A 6-cm diameter bucket auger was used to dig 5 holes in a concentric ring <1 m radius from the base of the shrub to a depth of 40 cm which coincided with the depth where the majority of millet roots were found. The soil was collected into one sample, transported to the lab, weighed, and then stored at 4 ºC for future root extraction.

**4.3.4. AMF colonization rates**

Fine millet roots, 1-2 cm long with an intact cortex, were picked from the entire surface area of the root system, thoroughly rinsed in distilled water, and stored in a 70 % (v/v) ethanol (EtOH) solution. Samples were prepared for AMF colonization rate determination following the methods of Phillips and Hayman, (1970). First, roots were rinsed in distilled water before the cytoplasm was cleared by immersing the roots in a 10% KOH soln. Next, they were placed in a 90 ºC water bath for 25 min. After the water bath incubation, roots were thoroughly rinsed with tap water over a 50 µm sieve for 1 min. and then transferred to glass tubes containing 0.05 % trypan blue soln. (0.5 g trypan blue powder, 100 ml vinegar, and 900 ml distilled water). Next the roots were
placed back into the 90 °C water bath for 20 min. After this, the roots were rinsed with water and mounted on microscope slides with glycerol (30 to 40 root fragments/slide). Each sample consisted of one or two slides. The percentage of the root length colonized by AMF hyphae, arbuscules, and vesicles/spores was determined under a compound microscope using the method of McGonigle et al., (1990) with modifications outlined by Schreiner (2003). Percent colonization was determined by dividing the number of AMF structures counted at each root grid intersection by the total number of root grid intersections.

Roots of *G. senegalensis* were picked from soil by the washing and sieving method outlined by Böhm (1979). Briefly, each sample (~ 4 to 5 kg fresh weight) was divided into 4 to 5 aliquots which were then placed one at a time into a 2 L bucket. Approximately 1 L of water was added to the bucket and the soil solution stirred vigorously for approximately 30 sec. before it was decanted onto a 500 µm sieve. Roots were transferred from the sieve in small batches to a petri dish with dH₂O, and fine, cream-colored primary roots with intact cortex were picked with tweezers, rinsed thoroughly in distilled water then transferred to 15 mL falcon tubes with 70% EtOH soln. for storage. Shrub roots were cleared, stained, and percent mycorrhizal colonization determined as above except that roots were cleared in KOH for 45 instead of 25 min.

4.3.5. Soil chemical characteristics

Soil pH was determined using a glass membrane electrode in a 1:2 soil:water solution. Analysis of total C and N was performed on an Elemental Analyzer 1108 (Carlo Erba Instruments, Milano, Italy). Plant nutrients: P, K, Ca, Mg, S, Fe, Cu, and Zn, were extracted using a Mehlich 3 solution (ammonium-fluoride-EDTA) (Mehlich, 1984),
followed by analysis on an ICP-OES 700 (Agilent Technologies, Santa Clara, CA)(USEPA, 2007).

4.3.6. FAME analysis

FAME analysis on 2013 and 2014 soil samples (2014 survey was identical to that described in section 4.3.3.) was conducted according to the methods of Shutter and Dick (2000). Three grams of soil were mixed with 15 ml of 0.2 M KOH at 37°C for 1 hour in a 35-ml centrifuge tube to induce mild alkaline methanolysis of the ester-linked fatty acids. Every 10 min the solution was mixed with a vortex for 10 seconds. After incubation, each sample was neutralized with approximately 3 ml of a 1 M NaOH soln. Next, 10 ml hexane was added, and the solutions were vortexed thoroughly followed by centrifugation to extract the FAMEs. Those collected in the hexane supernatant were dried via evaporation at 39°C under N₂ gas. Samples were then prepped for GC analysis by dissolution in 192 L 1:1 Hexane:MTBE and an 8 L MIDI internal standard. The FAME samples were analyzed with a gas chromatograph-flame ionization detector, with a 25 m, 0.2 mm diameter and film thickness 0.33 m, HP Ultra-2 column, with H and N as the carrier gas. The MIDI library was then used to match detected peaks of the sample to known fungal and bacterial biomarkers.

Fatty acids were extracted and quantified using MIDI Sherlock Microbial Identification System (MIDI, Newark, Delaware, USA). Peak areas of the fatty acids were converted to a molar unit using the following equation:

\[
\text{Concentration} \left( \frac{\text{nmol}}{\text{g}} \right) = \frac{F_{FM} \times c_{IS} \times 2 \times 1000 \times 100}{E \times W \times T \times S \times F_{IS} \times M_{G_{FM}}} \]

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where $F_{FM}$ is the area of the phospholipid methyl ester peak. $MG_{FM}$ represents the molecular weight of the phospholipid methyl ester in $\mu$g/µmol. $C_{IS}$ is the concentration of the internal standard in $\mu$g. $F_{IS}$ is the area of the internal standard. $EW$ is the mass of the soil in grams, and $TS$ is the dry matter of the soil in % ($100/TS = \text{dry matter factor}$). The variable factor of 2 is based on the volume of the extractant, and multiplying by 1000 converts $\mu$mol to nmol. In total, fatty acids from 22 groups of soil microorganisms were identified and summed for a total FAME number. The AMF fatty acid marker 16:1 $\omega$5c was used to identify the AMF communities (Olsson et al., 1995).

4.3.7. Spore Community Analysis

A dry season sampling was conducted two weeks before seeding in June, 2014, to assess viable AMF spore density and diversity both near and far from G. senegalensis at the start of millet cropping. At four randomly-selected shrubs, a shovel was used to dig 4 holes 90º apart and < 1m radius from the base of the shrub to a depth of 40 cm. Soil was collected along the exposed soil profile of each hole at 5 cm intervals to the 40-cm depth and homogenized into one composite sample. For the far shrub samples, 4 holes were dug approximately 90º apart and 5 m distance from the base of the shrub and 5 m from the base of any other shrub to form a composite sample. The dry soil samples dry—<1% volumetric water content in the field—were stored at room temperature before being transported to the USDA-ARS Horticulture and Crops Research Lab in Corvallis, OR, for spore identification.

AMF spores were extracted from 50 g (dry weight) of soil according to the wet-sieving/sucrose centrifugation method of Daniels and Skipper (1982). Briefly, samples
were placed into 1 L of tap water, thoroughly mixed and poured over a stacked set of 500 and 45 µm sieves. The process was repeated 2 more times. Material on the 45 µm sieve was then rinsed thoroughly and transferred to two 50 mL centrifuge tubes. The tubes were centrifuged at 7,000 rpm for 5 minutes and the supernatant decanted. Next, the pellet was re-suspended in a 50% (w/v) sucrose solution and the tubes centrifuged at 1750 rpm for 1 minute. Finally, the sucrose solution was decanted into a beaker of tap water and the spores caught and rinsed on a 45 µm sieve before being transferred to a petri dish with distilled water and observed under a stereoscope. The remaining pellet from the sucrose fraction and the portion of the sample caught on the 500 µm sieve were re-suspended in water, sieved through a 75 µm sieve and examined in petri dishes under a stereoscope.

All spores were divided into large and small fractions which were roughly greater or less than 150 µm in diameter respectively, and only healthy unparasitized spores with intact cell walls were counted to achieve a total spore density g⁻¹. The spores from one site in each region (B and Y) were examined first to aid in the characterization of the second site within each zone. All large spores were collected, counted, and those that had easily-identifiable, distinct morphological characteristics (size, shape, or coloring) were divided into 5 to 10 separate groups, rinsed in deionized water, photographed, and half the sample mounted on slides in polyvinyl-lactic acid-glycerine (PVLG) (Koske and Tessier, 1983) and the other half in a 1:1 (v/v) PVLG:Melzer’s reagent (Brundrett et al., 1994). The rest of the large spores were mounted together on miscellaneous slides. All slides were dried at 65°C overnight and examined under a compound microscope at up to 400-fold magnification. Species identification (when possible) was performed based on
taxonomic descriptions found in identification manuals (Schenck and Pérez, 1988, http://invam.wvu.edu/, http://www.zor.zut.edu.pl/Glomeromycota/, http://schuessler.userweb.mwn.de/amphylo/). When a positive species identification could not be obtained with confidence but there was consensus that the spore represented a distinct morphotype, the genus of the spore was noted with “unknown species.” For the Gigaspora genus, the authors noted several morphologies of at least 2 species, and consequently elected to group all spores in that genus as “Gigaspora spp.” Small spores were grouped under the stereoscope and approximately half were mounted on slides and identified using the methods previously described for large spores.

4.3.8. Statistical analysis

Statistics were performed in SAS (Version 9.4; SAS Institute, Cary, NC). The PROC GLM procedure was used to analyze AMF colonization and soil survey data from the 2013 rainy season. The PROC MIXED subroutine was used to analyze FAME data because the Akaike information criterion (AIC) for this model was higher for those data. The main effects were region, site, and location to shrub. A blocking factor was employed to group plant and soil samples from the same transect at the six shrubs/site. The significance of year was determined for FAME data from 2013 and 2014, but the model did not include repeated measures in time because although the same sites were used, samples were not necessarily taken from the same shrubs. Differences were considered significant at \( P < 0.05 \), and Tukey’s honest significant difference test was used to separate significant effects. Correlations between soil chemical characteristics, AMF root colonization, millet height and FAMEs were examined for 2013. A Chi-square test of independence was used for the 2014 dry season spore survey to test the hypothesis that
spore counts’ location to shrubs was independent of site or region. When the null hypothesis for independence was rejected, an ANOVA or Kruskal-Wallis ANOVA (when assumptions were violated) was performed to determine significant differences. ANOVAs were also used to identify significant differences by the shrub effect.

4.4. Results

4.4.1. Soil properties

Total C and eight of nine analyzed soil nutrients were significantly greater in the southern Sudanian zone (Table 4.1). In addition, all measured soil properties differed by site with either X or Y having the highest values. Moreover, except for Cu and Zn, there were significantly higher levels of extractable nutrients either in the center of the shrub rooting zone or in near millet plants <1 m from the shrub in at least one site. In total, the positive shrub effect (either ‘shrub’ or ‘near’ samples) on soil nutrients was significant for seven nutrients at the X site, four at the A site, one at the Y site, and for none at the B site. Interestingly, total C was significantly higher in shrub samples at sites A and X but not at B and Y. Table 4.2 shows a positive correlation between total C and all the other nutrients with an especially strong association with N ($r=0.96$) and Ca ($r=0.77$) and a robust one for P, S, Fe, and Cu ($r>0.60$). There was also a positive correlation between millet height at the Sudanian site and C, N, K, Ca, S, and Fe and a negative one with P and Cu. Soil pH was uniformly lower by at least 0.1 units in the shrub samples compared to the near and far samples (Table 4.1), and the differences were significant at sites A and B.

4.4.2. Millet sampling and AMF colonization
Millet height differed significantly both regionally and by site with taller plants in the northern zone (Fig. 4.2). However, plants growing <1 m from the base of *G. senegalensis* were taller than plants >5 m distance at every site. The blocking effect examining plants growing on the same transect was not significant. Millet fresh biomass was also significantly greater in near plants (*P*<0.0001) at all sites (data not shown).

AMF colonization rates were very high at the northern sites. Hyphae were found infecting 91% of shrub root length at the A site and 83% at the B site (Fig. 4.2). Colonization in the near millet plants at the A and B sites were 88 and 87% respectively and 89 and 83% in the far millet plants. At the southern sites, there was less hyphal colonization (*P*<0.0001) with 80 and 72% of the shrub root length infected at X and Y respectively, 59 and 50% colonization of near millet plants, and 70 and 50% colonization rates in far millet. Arbuscule and vesicle/spore colonization rates followed the same pattern as hyphae (*r*=0.73, Table 4.2) with a significant regional difference (Sahel>Sudan) and a significant difference by site (*P*<0.0001)(Fig. 4.2). Arbuscule colonization rates also tracked the hyphal colonization pattern where arbuscules were most prevalent in shrub roots at all sites with means of 65% in the Sahelian zone and 46% in the Sudanian zone. Near millet colonization was 53 and 31% in the two respective regions and 51 and 32% in far millet plants. Vesicle/spore colonization was significantly higher in near millet plants (57 and 53%) than in far plants (38 and 28%) or shrubs (32 and 26%) at the A and B sites respectively, but those were the only significant within-site treatment location differences other than greater hyphal colonization in shrubs at the Y site (Fig. 4.2). The block effect was not significant for any AMF structures or for millet height and biomass. Table 4.2 shows that, with the exception of K, there was a
negative correlation (sometimes not significant) between soil nutrients and AMF colonization. Millet height was also not correlated with AMF colonization structures rates except for arbuscules in millet at the Sudanian sites ($r=0.51$).

4.4.3. FAME surveys

Abundance of AMF FAMEs in 2013 closely followed the pattern of AMF intraroot colonization. Namely, the Sahelian zone had significantly greater AMF fatty acids than the Sudanian zone ($P=0.004$), and site A had a significantly greater abundance of AMF than sites X or Y (Fig. 4.3). There was, however, a very significant difference by year ($P<0.0001$) with a greater level of AMF FAMEs in 2013 than 2014. Nonetheless, in 2014 the northern region still maintained significantly higher levels of AMF than the southern region ($P=0.047$), though site B had the most FAMEs of all sites and was statistically greater than sites A and X (Fig. 4.3). Neither location to shrub nor the blocking effect were significant for AMF in 2013 or 2014. However, like colonization patterns in 2013, there were greater (though not statistically significant) AMF FAMEs at the base of the shrub than in near or far millet plants for sites A, X, and Y. The percentage of total FAMEs which were AMF from sites A, B, X, and Y were 14, 12, 9, and 9% respectively in 2013. In 2014, AMF FAMEs comprised 6, 10, 4, and 6% of the total.

Corresponding with the AMF FAME data, there was no significant shrub or blocking effect on total FAMEs. Site and region were also not significant for 2013, and there was no difference between 2013 and 2014 for total FAMEs ($P=0.25$). However, the effect of site was significant in 2014, and B was greater than sites A or X (Fig. 4.3). Correlations between AMF or total FAMEs and soil characteristics were not significant,
and only arbuscule colonization was slightly positively correlated with AMF FAMEs (Table 4.2). Millet height in the Sahelian zone was also slightly positively correlated with the levels of AMF FAMEs.

4.4.4. AMF spores

Spore density was low in the two weeks before the start of the 2014 rainy season: 3.3, 5.1, 4.2, and 7.5 spores g$^{-1}$ at sites A, B, X, and Y respectively (Table 4.3). The primary driver of spore abundance was site, with significantly more spores at Y than at A and X. Regional differences were also nearly significant ($P=0.051$) with more spores in the Sudanian zone than in the Sahel. Overall, twelve genera from five families were represented in this survey (Table 4.3). However, five genera (Racocetra, Dentiscutata, Gigaspora, Glomus, and Acaulospora) comprised >90% of the relative species abundance at sites B, X, and Y and >83% of the abundance at site A (Fig. 4.4).

Acaulospora was the most abundant genus at all sites. Twenty-four distinct morphotypes were distinguished in the survey, and sixteen morphotypes were positively identified to the species level (Table 4.3). Nevertheless, only four species comprised >50% of the relative species abundance at all four sites. A. dilatata was the most prevalent species and constituted 24, 32, 35, and 43% of the relative species abundance at A, B, X, and Y respectively. A. mellea and D. heterogama were either the second or third most abundant species for A, B, and X, and A. mellea and R. fulgida were the second and third-most abundant species at site Y.

The large chi square statistic for all but two species suggests that there was a relationship between proximity to the shrub and site (Table 4.3). However, location to shrub was independent of region for sixteen of the 24 morphotypes (data not shown).
The ANOVA showed significant differences between near and far shrub spore samples for three species: *D. heterogama, R. fulgida,* and *R. verrucosa* (Table 4.3). However, it was only a positive effect near the shrub for *D. heterogama.* Species richness was not significantly different near or far from the shrub (Table 4.3). Nevertheless, site Y, with a species richness of fourteen, was significantly greater than sites A and B, both with a species richness’ of twelve. In total, twelve morphotypes were found in >50% of all samples, and nine morphotypes (*A. dilatata, A. leptoticha, A. mellea, D. heterogama,* *Gigaspora* spp., *G. ambisporum, R. fulgida, R. gregaria,* and *R. verrucosa*) were in ≥75% of samples. All morphotypes from the Gigasporaceae and Acaulosporaceae (eleven total) were represented in the majority of samples with the exception of *Scutellospora cerradensis* and one unknown *Acaulospora* morphotype. The grouped *Gigaspora* spp. was the only morphotype found in 100% of samples.

4.5. Discussion

4.5.1. AMF in agroforestry systems of the WAS

This research comes at a critical juncture for the WAS where the demands of rapid population growth and climate change are increasing the demands for climate smart agricultural systems which can simultaneously increase food security and mitigate threats from changing weather patterns (Lipper et al., 2014). Agroforestry systems are suggested as viable options both for enhancing productivity and improving soil C sequestration (Bayala et al., 2014; Lal, 2004; McIntyre, 2009). In the WAS, the natural woody vegetation provides multiple ecosystem services and a principal benefit is their ability to improve soil fertility (Bayala et al., 2015; Sinare & Gordon, 2015). AMF communities
play a fundamental role in facilitating this increased soil fertility through their uptake and redistribution of soil nutrients as well as the prevention of nutrient losses (Cavagnaro et al., 2015; Courty et al., 2015; Smith & Smith, 2011; van der Heijden & Horton, 2009). Furthermore, on average, 5-10% of soil organic carbon is derived from glomalin deposition by AMF (Xu et al., 2017), and consequently this fungal phylum also plays an important role in C sequestration (Wilson et al., 2009). Therefore, the lack of basic research on AMF ecology in shrub-intercropping systems of the WAS represents a significant knowledge gap for the understanding and effective management of climate smart agricultural systems. This study was conducted to address that need.

4.5.2. Root colonization dynamics

Root colonization of pearl millet in this survey was higher than rates from other field experiments in the WAS. Hafner et al. (1993) was the first to examine colonization of millet roots and found levels ranging from 15-60% in sandy soils of Niger. Bagayoko et al. (2000) reported 11-64% AMF colonization at three sites in Niger and Burkina Faso with significantly higher infection rates in millet succeeding a cowpea rotation than in a continuous-cropping system. In both of those studies, however, (and also in another survey in Niger and Burkina Faso by Alvey et al., 2001), colonization significantly increased over the duration of the cropping season. In this study, plants were sampled at approximately 75-90 days after sowing (DAS) for sites A and B and at approximately 60-80 DAS at X and Y. The results suggest, therefore, that greater colonization in the Sahelian region can be partially explained by differences in the physiological age of the plants. Moreover, colonization rates were only examined during one growing season. In contrast, Hafner et al. (1993) evaluated colonization over two rainy seasons and found
very significant differences by year: 15-20% colonization in the first and 55-60% in the next. Thus, there is a high probability that colonization in the *G. senegalensis*-millet intercropping system is highly dependent on interannual abiotic factors.

In conjunction with millet, *G. senegalensis* roots were highly colonized in this survey. To the best of our knowledge, Ibrahim et al. (1995) were the first and only other authors to examine AMF ecology in *G. senegalensis*. They found low-level colonization (<10%) in a high number of shrubs across southwest Niger. However, the high AMF infection in *G. senegalensis* from our study was consistent with rates found in other ubiquitous agroforestry species across the region. For example, *Faidherbia albida* (syn. *Acacia albida*) rates were between 50 and 80% in the Sahelian and Sudanian zones of Senegal (Diop et al., 1994), and the authors found no significant differences between ecological zones. Dalpé et al. (2000) also found colonization rates >50% in *F. albida* tree roots in Senegal. Tomlinson et al. (1995) noted 85% infection of *Parkia Biglobosa* at two sites in the Sudanian region of Burkina Faso. Four trees used for alley cropping in central Senegal: *Acacia tortilis, A. nilotica, A. aneura,* and *Prosopis juliflora,* had infection rates between 31 and 66% (Diagne et al., 2001; Ingleby et al., 1997). In *P. reticulatum* intercropped with mango trees (*Mangifera indica*), Hernandez et al., (2015) found that 55% of the root length was colonized. Finally, Duponnois et al. (2001) studied AMF ecology in different woody species from fallows in the Saloum of Senegal and described infection rates between 6 and 92%.

There is evidence that that higher infection rates in millet enhanced P uptake in a pot experiment using soils from Niger (Beggi et al., 2016). Another study, however, examined the effect of 23 agroforestry trees on soil fertility and AMF dynamics in
Senegal and found no relationships between the three components (Bernatchez et al., 2008). In this field study, it is unclear whether high levels of AMF colonization in millet and *G. senegalensis* roots adjacent to them indicate a beneficial growth effect and furthermore to what extent (Smith & Smith, 2015). Nevertheless, there are three important beneficial aspects of the symbiosis for improved millet growth in the rooting zone of *G. senegalensis*. First, AMF mycelia (the collective mass of hyphae in the soil) expand the effective root length density of plants and consequently their ability to take up nutrients and water (Augé, 2004; Schroth, 1999). Thus, there is a positive relationship between root infection and effective root length density. Van der Heijden et al. (2015) found that when 15% of the root length was colonized, the effective root length density increased by a factor of approximately 2.5. Second, plants transfer up to 20% of photosynthetically-fixed C to their AMF symbionts (Parniske, 2008) which can increase not only soil C but also extractable nutrients in the soil that are associated with organic molecules. Thus, high levels of hyphal colonization in both millet and *G. senegalensis* indicates putative high levels of soil mycelia which could increase overall fertility, facilitate nutrient cycling, and enhance millet growth. Third, the great majority of plants can connect with multiple AMF species, and this lack of specificity combined with high colonization in both shrub and millet roots suggests the likelihood of a common mycorrhizal network (CMN) between them (Simard et al., 2012).

4.5.3. Benefits of a putative common mycorrhizal network

The putative presence of a CMN in this intercropping system is especially important for agroecosystem function in the WAS. Research has shown that N and other nutrients can be transferred from a donor to a receiver plant even if the donor plant does
not fix N (Fellbaum et al., 2014; Teste et al., 2015). The CMN is important for seedling establishment (van der Heijden & Horton, 2009). Millet seedlings could receive hydraulically-lifted water from *G. senegalensis* that is helping them survive during times of drought (Egerton-Warburton et al., 2007; Prieto et al., 2011) which are expected with increasing frequency in the WAS (Dai, 2013; Xue et al., 2016). Finally, the CMN is important for interplant signaling which induces important defense mechanisms against insects and other microbial pests (Johnson & Gilbert, 2015). High colonization in millet far from the shrub might also indicate the presence of CMNs formed between those plants and the herbaceous weed communities which the authors observed with a high frequency in bare patches between shrubs. Future studies should examine not only the presence or absence of CMNs between millet and *G. senegalensis* but also their presence between millet and weed communities. Furthermore, these studies should examine mechanisms of nutrient and water transfer (especially HL water) between plants via the CMM and to what extent the CMN facilitates commensalism, parasitism, or mutualism.

### 4.5.4. FAME analysis

The 16:1 ω5c fatty acids are a component of both AMF hyphae and spores (Madan et al., 2002; Olsson & Johansen, 2000). Yet, external mycelia comprise the majority of the AMF soil biomass (Olsson et al., 1995, 1997), and the 16:1 ω5c is correlates highly with AMF soil hyphal density which suggests that the AMF FAMEs in this experiment primarily represent the mycelial network (Olsson et al., 1995). Nevertheless, external AMF hyphal architecture is very complex with different species exhibiting different growth and branching strategies (Friese, 1991; Parniske, 2008). Furthermore, hyphae can experience rapid turnover rates in soils (Querejeta et al., 2007),
and some spores can also germinate in the absence of plant host signals (Sbrana et al., 2011). The combination of these factors conveys a large degree of expected variability in the levels of AMF FAMEs from an ecological survey in a semi-arid region, and the data from 2013 and 2014 bear that out. FAMEs from 2014 were significantly lower than in 2013, however, rainfall in 2014 was lower than in 2013 for the Sudanian region (Bright et al., 2017) which certainly could have decreased mycelial networks. Sampling also occurred earlier in the cropping season. The relative lack of correlations between intraroot colonization and FAMEs suggests that networks in the soil might either be fairly constant or turnover rapidly, and/or that plant dynamics controlling the internal and external AMF dynamics are quite different. Importantly, however, the concentration of AMF fatty acids as a percent of the total was much higher at all four sites in both 2013 and 2014 than AMF concentrations reported in arable or forest soils in a review by Joergensen and Wichen (2008). This again indicates the importance of the AMF symbiosis to agroecosystem function in this region.

4.5.5. AMF spores in the G. senegalensis-millet intercropping system

Approximately ten papers have examined AMF spore communities in the WAS. However, to the best of our knowledge, no papers have assessed AMF spores in the G. senegalensis rooting zone nor have any identified the communities specific to millet production. Spore abundance from the four sites both near and far from shrubs in this survey were higher than most densities recorded in the region. Only Duponnois et al. (2001) found higher densities (209 spores/50 g or 4.2 g⁻¹ in fallow systems of Senegal) than two sites in this survey. Other papers evaluated spores near to agroforestry species
and found very low abundances of <50 spores/50 g soil (Hernandez et al., 2015; Ingleby et al., 1997; Sene et al., 2012a,b).

In this survey, AMF species’ richness was more than two times greater than other field studies from the WAS. Both Remigi et al. (2008) and Sene et al. (2010) found nine species from the rooting zones of trees in central Senegal. The other articles recorded <4 species/site (Duponnois, 2001; Ingleby et al., 1997; Sanon et al., 2009). Thirteen of the sixteen positively-identified species from this study were novel in the WAS. *G. aggregatum* was the most ubiquitous species in the region: found at all four sites in this survey and at three other locations in Senegal (Dalpé et al., 2000; Remigi et al., 2008; Sene et al., 2012a). *R. verrucosa* and *R. gregaria* were the other two species discovered both in this study and from two other sites in Senegal. Other studies noted a heavy presence of *Glomus* species (Duponnois, 2001; Ingleby et al., 1997) and specifically the presence of *G. intraradices* at two locations (Sanon et al., 2009; Sene et al., 2012a).

Interestingly, only Bourou et al. (2010) mentioned the *Acaulospora* genus, and the other studies only recorded species from three genera: *Gigaspora, Scutellospora*, and *Glomus*.

Spores in this study likely represent an underestimation of species richness and abundance because it is unlikely that all species sporulated at the time of sampling (Bever et al., 2001; Sanders, 2004). For example, Diop et al. (1994) found 262% more viable spores during the rainy season than the dry. Some species infrequently, if ever, sporulate (Douds & Millner, 1999). Moreover, spore viability is often very low (McGonigle & Miller, 1996), and degraded spores are not suitable for identification. In addition, the Gigasporaceae propagate mainly by sporulation, whereas the Glomeraceae often rely on extraradical hyphae to infect plants (Smith & Read, 2008). Consequently, the species
richness in the soil does not necessarily represent richness in the roots of *G. senegalensis* or millet. In their study examining AMF ecology in the rooting zone of four agroforestry species of the WAS, Ingleby et al. (1997) found that with the exception of *Acacia aneura*, there was no correlation between spore density and mycorrhizal colonization. They concluded that because soil disturbance is low in these sandy ecosystems of the Sahel, root colonization happens primarily from hyphal networks and senescing AMF roots. More studies using molecular techniques are needed to compare intraroot colonization dynamics between *G. senegalensis* and millet with soil spore communities (Öpik et al., 2014). Nevertheless, though cumbersome, identification of AMF communities using spore morphology retains ecological significance and importance (Öpik & Davison, 2016) especially since community composition changes between roots, mycelia, and spores (Varela-Cervero et al., 2015). The high levels of AMF species abundance and richness observed in this study are important for ecosystem function and are also assumed to be a precondition of sustainable cropping systems (Mäder et al., 2002).

### 4.5.6. Soil nutrients and millet height

Importantly, this study again showed the strong, beneficial effect of *G. senegalensis* on millet growth (Debenport et al., 2015; Dossa et al., 2012; Kizito et al., 2006). Moreover, the effect was not confined to a single location but rather was distributed across the Sahelian and Sudanian zones. This has not been shown before. The higher levels of soil nutrients and C in the shrub rooting zone also confirm that *G. senegalensis* increases soil fertility across the region and not just at single sites as was observed in previous studies, (Dossa et al., 2008; Dossa et al., 2009; Lufa fait et al., 2008a,b). In addition, the positive correlations between C and the other nutrients suggest
that a chief benefit of shrubs across the landscape is their ability to increase soil organic C and mineralization rates. As discussed in section 4.5.2., the AMF are heavily involved in soil C cycling and consequently could be directly responsible for increased nutrient levels near the shrubs.

4.6. Conclusions

An assessment of AMF community structure and dynamics is a necessary precondition both to understand the symbiosis and to identify beneficial effects imparted by specific species. This research, therefore, represents an important first step in understanding AMF ecology between *G. senegalensis* and pearl millet and lays the foundation for future mechanistic studies. Moreover, this study contributes to the literature on basic AMF ecology in the WAS by identifying thirteen previously unrecognized species and a total richness more than double what was recorded in other surveys. The results confirm that the beneficial effect of *G. senegalensis* on soil fertility and millet growth was not limited to one location but rather was distributed across the rainfall gradient. As a result, these data combined with evidence that *G. senegalensis* densities are increasing in the WAS again support the suitability of this shrub for use as an agroforestry species to increase food security.

Though the shrub did not have a significant effect on most AMF dynamics (spore abundance, FAMEs, species richness, or colonization), nevertheless the high colonization rates and FAMEs in the intercropping system suggest that a putative CMN exists between plants. The greater soil fertility in the shrub rooting zone also suggests that the turnover of AMF mycelia in addition to secretion of glomalin and other organic molecules is a
driver of enhanced millet growth. Consequently, there is a potential positive AMF feedback loop in the the *G. senegalensis* rooting zone where mycelial growth and senescence increase nutrient levels which can then be taken up by other mycelia and transferred from shrub to millet through the CMN. Higher levels of FAMEs and colonization in the drier Sahelian zone further indicate the importance of the AMF symbiosis to millet growth in the WAS. The fact that few farmers use synthetic fertilizers or deep tillage suggests that increasing the densities of *G. senegalensis* is an effective strategy for extending the positive beneficial effects of AMF.

4.7. References


Agriculture, Ecosystems & Environment, 205, 25-35. 
doi:10.1016/j.agee.2015.02.018


doi:10.1016/j.jaridenv.2007.12.014


doi:10.1016/j.agee.2017.03.007


Sanders, I. R. (2004). Plant and arbuscular mycorrhizal fungal diversity - are we looking at the relevant levels of diversity and are we using the right techniques? *New Phytol, 164*, 415-418.


Table 4.1. Soil nutrients, pH, and total C in the center of *G. senegalensis* canopy (Shrub), next to millet growing within the rooting zone of the shrub (Near), and in millet >5 m from the shrub (Far) at the 4 survey sites in Senegal, West Africa.

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<tr>
<th>Soil Nutrients</th>
<th>Ndiaye Thioro (A)</th>
<th>Khoyele (B)</th>
<th>Thiarene (X)</th>
<th>Paoskoto (Y)</th>
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<td>Far</td>
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<td>Zn*</td>
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**Assorted Chemical Properties**

| pH              | 5.51b  | 5.65a | 5.76a | 5.62b  | 5.81a  | 5.73ab | 5.51a  | 5.54a  | 5.67a | 5.66a  | 5.72a  | 5.78a |
| Total C (%)*    | 0.21a  | 0.13b | 0.09b | 0.14a  | 0.14a  | 0.11a  | 0.34a  | 0.33a  | 0.25b | 0.30a  | 0.28a  | 0.25a |

* Indicates a significant difference between Sudanian (X,Y) and Sahelian (A,B) regions.
† Within sites, values that share the same letter are not statistically different (*P*<0.05).
Table 4.2. Table 2. Correlation matrix showing associations between soil biological and chemical variables.

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* Signifies a model with a P-value <0.05.
§ “Height Sud.” represents the height of millet plants from the Sudanian Region (X and Y) and “Height Sah.” the Sahelian (A and B).
Table 4.3. Spore abundance and diversity at 4 survey sites in the Sudanian and Sahelian zones of Senegal, West Africa.

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<th>Far</th>
<th>Mean</th>
<th>Near</th>
<th>Far</th>
<th>Mean</th>
<th>Near</th>
<th>Far</th>
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* Indicates a significant difference by site, and ** indicates a significant difference by location to shrub.
Figure 4.1. Location of four sites (represented by stars) used for surveys in the Sahelian (northern) and Sudanian (southern) ecological zones of Senegal.
Figure 4.2. Arbuscular mycorhizal fungal (AMF) colonization rates and millet height in shrubs and millet plants near (<1 m) and far (>5 m) from the base of the shrub at the four sites in Senegal. Bars that do share the same letter are not statistically different. Error bars are SEM.
Figure 4.3. Total and AMF FAMEs from 2013 and 2014 surveys at the survey sites. Sites that share the same capital letter are not statistically different.
Figure 4.4. AMF genera represented at the four survey sites. “Other” represents *Ambispora, Archaeospora, Claroideoglomus, Funneliformis, Rhizophagus, Sclerocystis,* and *Scutellospora.*
Chapter 5: A Review of the Uses, Ecology, and Agroforestry Potential of Shrubs in the West African Sahel

5.1. Abstract

The term ‘agroforestry’ typically connotes planting crops next to trees. Nevertheless, in the West African Sahel (WAS) where shrubs comprise a dominant component of the natural savanna vegetation, the term also signifies planting crops next to shrubs. In comparison with the literature and reviews on trees in the WAS, relatively few studies examine shrubs, and there are no reviews. Therefore, the purpose of this paper is to summarize the research on shrub dynamics in the WAS including, diversity, densities, growth habits, ecosystem services, socioeconomics, and agroforestry potential.

Overall, the literature indicates the eminent suitability of shrubs for agroforestry in the region. Two shrubs in particular—*Guiera senegalensis* and *Piliostigma reticulatum*—have growth habits and phenotypes that uniquely adapt them to intercropping. Although most shrubs lack the intrinsic economic value of trees and do not produce edible fruits, the majority are useful for animal fodder and firewood. They also extensively reduce wind and water erosion. Thus, shrubs stabilize and build soil which prevents land degradation and provides a better growth habitat for trees. Their abundant biomass production combined with high densities suggest that there is a large potential for carbon sequestration in shrub-based agricultural systems.
The mechanisms behind the benefits of shrubs are: a) increased nutrients and carbon near the shrub canopy which improve chemical, physical, and biological properties of soil, b) spatial and temporal offsets of water use from crops, c) recruitment of beneficial microorganisms to increase nutrient cycling, d) low growth habit and lack of shading, e) ability to withstand coppicing, and f) vegetative regeneration from stems, fast establishment, drought tolerance, and hence, abundant biomass production. Recent research suggests that shrub densities are increasing across the WAS due to a combination of anthropogenic pressures including grazing and expanding croplands, and droughts and increasing temperatures from climate change. Thus, intercropping systems that incorporate shrubs systems are well-suited to the constraints and needs of the region and should be used in development programs (e.g., the Great Green Wall Initiative) that seek to prevent land degradation in the WAS. This review also examines future avenues of research for shrub-based agroforestry.

5.2. Introduction

Savanna vegetation—a mixture of trees, shrubs and grasslands—typifies the West African Sahel (WAS). In Senegal, it occupies approximately 70% of the land surface (Woomer et al., 2004). Moreover, the woody canopy covers an average of 7% of the ground (at the 1-km scale): from 2% in the northern drier extremity to 15% in the humid south (Brandt et al., 2016). In reality, the WAS is far from a homogeneous tapestry of grasses intermingled with woody species. Under the broad savanna classification, different ecoregions exist with characteristic vegetation types that are a function of the soils, geomorphology, and local weather patterns. For example, Tappan et al. (2004) and
Frederiks and Erik (1992) specify seven categories based on the predominant flora and growth patterns: wooded grasslands, open steppes, shrub steppes, open shrub steppes, shrub savannas, bushlands, and tree savannas. Subdividing the categories designates the very specific growth habits of shrubs in steppes and bushlands. One example is the so-called ‘tiger bush’ (brousse tigrée in French) which describes the alternating banding pattern of shrubs with strips of bare soil in between: an ecological adaptation of shrubs to sandy, degraded soils in drylands (Barbier et al., 2008; Couteron et al., 2000; Müller, 2013).

The two main agricultural occupations in the region, crop production and animal grazing, result in a mosaic of land use practices that center on the use of savanna vegetation. Consequently, the WAS is predominantly characterized by rangelands, cultivated lands, fallows, and parklands. Woomer et al. (Woomer et al., 2004), reported that cultivated lands comprise 22% of Senegal. Traditionally, there was a clear distinction between lands for crops (including parklands and fallows) and rangelands (Powell et al., 1996). However, the boundaries have become more fluid recently with drought-induced crop failure and rising population density forcing some farmers to engage in livestock production and vice versa to supplement their incomes (Bayala et al., 2014). Animal and crop husbandry are now increasingly linked in the WAS.

The woody savanna vegetation of the region further cements ties between crops and animals because farmers and pastoralists both depend on in it to sustain livelihoods in a system known as parkland agroforestry. Parklands are formed when crops are grown next to scattered trees and shrubs, which farmers preserved when they cleared their fields of natural woody vegetation in order to grow crops (Bayala et al., 2014). This adaptation
of the natural savanna ecosystem has been used for centuries and is the predominant agricultural system in the WAS (Bayala et al., 2015; Pullan, 1974). The preserved trees and shrubs are often used for animal fodder, or they provide other marketable products and ecosystem services (e.g. fruits, medicine, firewood, soil fertility) that make them valuable (Sinare & Gordon, 2015). Bayala et al. (2011) studied the parklands around twelve villages in central Burkina Faso and found 96 to 102 woody species (trees and shrubs). However, most of those species had fewer than ten individuals, and species richness decreased with proximity to the village, indicating the role of human selection on woody species. Lykke et al. (2004) reported 56 woody species and their uses in the northern Sahel of Burkina Faso. In a review of ecosystem services provided by the woody vegetation in the WAS, Sinare and Gordon (Sinare & Gordon, 2015) described only 30 species that were both ‘dominant’ and ‘common.” Furthermore, in a comprehensive review of parklands in the WAS, Pullan (Pullan, 1974) noted that only four species of trees dominate most of the parklands: *Andansonia digitata* (baobab), *Faidherbia albida* (winter thorn) *Vittelaria paradoxa* (shea), and *Parkia biglobosa* (locust bean).

Trees unequivocally benefit livelihoods in the WAS. Reij and Garrity, (2016) found that revenue from the sale of tree products accounted for 24% of the total household income in Burkina Faso and 7-10% of total household incomes in Mali, Niger, and Senegal. One mature baobab tree can generate from 34 to 75 US$ ha$^{-1}$ of annual income for a family in Niger which would enable them to purchase 70-175 kg of grain at local markets (Yamba & Sambo, 2012). Firewood also provides substantial income for many households, and most farmers also directly consume tree products for food (Place
Other major uses for parkland trees are as a fodder source, for medicine, and for crop production (Bayala et al., 2012, 2014; Sinare & Gordon, 2015).

In the WAS, farmer-managed natural regeneration (FMNR)—the suite of practices used to protect native trees in the parklands—has been successfully adopted in certain regions (Reij & Garrity, 2016). Haglund et al. (2011) estimated that FMNR has already added 900,000-1,000,000 trees to the WAS, and that the practice raised the gross annual income of the region by 17-21 million USD. Nevertheless, there are certain indications that FMNR practices might not be well-suited to the demands of increasing crop production in the region. The first challenge: Gijsbers et al. (Gijsbers, 1994) noted that maintaining fruit trees in the parklands requires farmers to water and protect young plants from livestock browsing during the dry season. The second challenge: trees often outcompete crops for water, nutrients, and light thus decreasing yields underneath their canopies (Bayala et al., 2012, 2015; Kessler, 1992; Smith et al., 1998). The third challenge: farmers are sometimes hesitant to plant trees because they take a long time to establish and need at least five years for a return on investment (Etongo et al., 2015; Lamers et al., 1994). In fact, Stoate and Jarju (2008) conducted an eight-year study in order to understand farmers’ perceptions of parkland trees and found that most of them recognized little value for using trees to increase yields. The fourth challenge: trees usually have very low densities across the WAS. Bayala et al. (2014) said that trees are typically maintained at fewer than 20 ha⁻¹ in the parklands; Sinare and Gordon (2015) described densities ranging from 2 to 55 trees ha⁻¹; and Pullan (Pullan, 1974) noted a maximum density of around 140 ha⁻¹. Thus, if the beneficial effect of trees on soil nutrients is largely confined to the canopy area (Bayala et al., 2015), then trees might not
be the best means to scale nutrient increases across large areas. The fifth challenge: the threat of climate change and pressures arising from increasing population density.

Researchers have described the Sahel as an unstable but resilient ecosystem (Brandt et al., 2017) that responds to dynamic changes in climate, vegetation, and anthropogenic land use (Herrmann et al., 2005). Over the course of the past century, the region has experienced severe droughts, specifically those in the 1970s and 1980s, followed by periods of increased rainfall (Nicholson, 2001). Changes in vegetation accompanied the climate variability. For example, Gonzalez et al. (2012) noted nearly 20% declines in both tree densities and species’ richness from 1954-2002. Vincke et al. (2010) reported a similar degradation of woody cover in northern Senegal between 1976 and 1995. Maranz (2009) also described a widespread disappearance of parkland tree species in the WAS. Nevertheless, the Sahel has experienced a ‘re-greening’ (overall increase in vegetation) during the past twenty years (Brandt et al., 2015; Kaptué et al., 2015). Despite the re-greening, there have been significant regional changes in vegetation dynamics (including localized diebacks) which are a result of human land use decisions (Brandt et al., 2014, 2015, 2016; Herrmann & Tappan, 2013). One of the principal changes to the native ecosystem has been a decrease in vegetation dominated by large trees and a concomitant increase in vegetation characterized by woody shrubs (Hänke et al., 2016; Herrmann & Tappan, 2013; Hiernaux et al., 2009; Lykke, 1998). The fact that shrubs are increasing despite anthropogenic pressures, that they retain many of the essential characteristics of trees, and that their short growth habit ipso facto reduces shading on crop plants, suggests a priori that shrubs species are best suited for parkland agroforestry in the WAS.
Across the globe, shrub encroachment is often synonymous with land degradation (Allington & Valone, 2010; MEA, 2005). The reason is that shrublands encroach on grasslands used for grazing. A simple model of this ecosystem conversion posits that overgrazing and concurrent protracted aridity cause grasses to die back and erosion events to occur which remove soil nutrients and leave the soil surface bare for colonization by shrubs. With their extensive root systems (both vertical and lateral) that make them extremely efficient users of soil water, shrubs spread across the landscape. Woody savannas in the WAS, with patches of shrubs and bare soil in between, has been described as ‘degraded’ (Bégué et al., 1994). Moreover, Le Houerou (1989) noted that large concentrated densities of shrubs are generally viewed as an indication of degradation. In contrast, Eldridge et al. (2011) reviewed the global impact of shrubland expansion on ecosystem function using 244 case studies worldwide. Their findings did not support the universal claim that shrub encroachment on grasslands is synonymous with degradation. Rather, they found that some positive ecosystem attributes such as soil carbon (C) and nitrogen (N) consistently increased with shrub encroachment.

This suggests that the increasing shrub densities in the WAS (Herrmann & Tappan, 2013) might be beneficial to the crop production and animal husbandry that are foundational to livelihoods there. Furthermore, there is a high potential to increase soil C levels in the WAS by using technologies that restore degraded lands (Tschakert et al., 2004). The potential exists because the natural levels of soil organic matter are extremely low and the land area in the WAS is extremely high. Shrubs could therefore be adapted to climate smart agricultural systems that increase food security while buffering against climate change (Lipper et al., 2014).
The overall objective of this review is to assess the literature describing the agricultural potential, ecology, management, benefits, and socioeconomic implications of shrub use in the WAS. Though other authors have reviewed aspects of the general woody vegetation in the region which included some shrubs (Bayala et al., 2014, 2015; Mbow et al., 2014; Sinare & Gordon, 2015), none has reviewed shrubs as distinct from trees. This review comes at a particularly important time because wide-scale initiatives such as the Great Green Wall are being promoted to combat land degradation and mitigate the threat of climate change in the WAS. These initiatives primarily focus tree planting strategies and other conservation agriculture technologies. This paper, therefore, addresses the use of shrubs as adaptable technologies to prevent further regional land degradation. Finally, future research directions for the development of enhanced shrub agroforestry systems are discussed.

5.3. Methods

5.3.1. Designation of shrubs and the species included in this review

The question—“What is a shrub?”—poses a challenge for any review of this subset of the woody vegetation in the WAS. Throughout the literature, many researchers use the terms ‘shrub’ and ‘tree’ interchangeably. Both words can also be used to refer to the same species over the course of one article which further complicates the issue. For example, in their survey of plant communities from the fallows of Niger, Wezel and Boecker (1998) refer to Combretum glutinosum as both a tree and a shrub. Even species which are almost universally acknowledged as ‘shrubs’ in the literature (e.g. Guiera senegalensis) are still sometimes called ‘trees’ (e.g. Geiger and Manu, 1993).
Occasionally, the classification arises from the habitat or land-use where the current woody species is found. For example, authors typically refer to species found in a fallow system as shrubs. And sometimes the usage references the morphology of the species; e.g., a smaller woody plant looks more like a shrub than a tree and therefore might be referenced as a shrub. More often, though, either the designation appears to be an arbitrary decision on the part of the individual author.

For this review, we adopted the definition of shrubs and trees used by Leenders et al. (2007). Namely, shrubs have multiple aboveground woody stems, whereas trees have a distinct trunk below a canopy and are also typically taller than shrubs. We consulted two widely-used botanical reference guides for a comprehensive list of shrubs in the WAS. The first was by Arbonnier (2004) and the second by von Maydell (1986). Many species in those guides are classified as ‘shrubs’ or small ‘trees.’ Nevertheless, we chose to include all species with a designation of ‘shrub,’ regardless of an overlapping tree identification, because many of the species classified as a ‘shrub or tree’ by Arbonnier (2004), e.g. *Piliostigma reticulatum*, are unambiguously called shrubs in the majority of the literature. Another rationale for being liberal with the ‘shrub’ designation is that well-studied trees in the WAS: e.g., *F. albida, P. biglobosa, V. paradoxa, A. digitata,* and *Balanites aegyptiaca,* are never confused with shrubs in the literature. Consequently, we were more concerned with false negative than false positive shrub identifications. Nonetheless, shrubs that are included in this review and which also bare a ‘tree’ designation by Arbonnier (2004), are noted in Table 5.1.

This study focuses on the Sahelian ecological zone. Consequently, shrubs were only considered if they are distributed in the Sahelian or Sudano-Sahelian subregions.
receiving 200-400 and 400-600 mm annual rainfall respectively (Le Houerou, 1980).

However, we chose to include shrubs predominant in more humid or drier regions but which overlap with the Sahelian zones because the regional weather patterns fluctuate markedly from year to year. Consequently, in any given year it would be difficult to constrain one species to rainfall boundaries between 200-600 mm. Nevertheless, to meet the requirements of this review, a shrub had to have a distribution that extended over either the Saharo-Saharan, Sahelian, or Sudano-Saharan zones recorded by Arbonnier (2004). Species that were classified as solely Sudanian, Saharan, or Guinean habitat were not included. Thus, this review omits some well-studied shrub species, such as *Piliostigma thonningii*, which belong to the Sudanese and Guinean savannas.

Furthermore, studies in this review were only included from the West African countries of Burkina Faso, Mali, Mauritania, Niger, and Senegal. Nigeria was excluded because very few studies have been conducted in the far north of that country, and that is the only region that is part of the WAS.

Though the majority of shrubs in this review are native to the WAS, this was not a requirement for inclusion (Table 5.1). The reason was that it is difficult to determine the origin of many species found in this study, and furthermore, an objective of this review is to determine beneficial uses for shrubs, such as agroforestry and carbon sequestration. Thus, in the view of these authors, it was counterproductive to exclude species perceived as ‘non-native.’ Finally, a few shrubs are not found in botanical reference guides, but are nonetheless described by other authors as important species for the region (e.g. *Diospyros lycioides* in (O'Connor and Ford, 2014)). In total, 64 shrubs met the criteria described in this and previous paragraphs (Table 5.1).
5.3.2. Literature review process

To capture the literature pertinent to the objectives of this review on shrubs in the WAS, we conducted a two-part search in the ISI Web of Science. The first part consisted of entering the Latin names (genus and species) of all 64 shrubs. The search was accomplished over the month of May, 2017. For non-native shrubs with wide distributions in Central or East Africa, Asia, or the Middle East, the following search string was added to the shrub’s latin name to reduce the number of unrelated publications: genus species AND (sahel* OR west africa*). The search yielded 2229 references.

The second part of the search process used terms intended to capture any general literature on shrubs without regard to species. Accordingly, on May 28, 2017, the following search string was entered into Web of Science: (shrub* OR scrub* OR bush* OR wood*) AND (sahel* OR west africa* OR senegal OR mauritania OR burkina faso OR niger* OR mali). Certain articles overlapped with those from the first search. Notwithstanding, the second part of the process yielded 3256 references.

We employed the following criteria to screen all titles and abstracts: 1) The study was conducted within the previously-mentioned 5 countries of the WAS; 2) The study took place approximately within the Sahelian or Sudanian ecological zones and not within a region clearly outside of their boundaries (e.g. the Cassamance of Senegal); 3) The study was not from a national park or protected forest reserve (e.g. Niokolo National Park or Bandia Forest Park in Senegal); 4) The study was not solely focused on a shrub product (e.g. fruit quality or the chemical structure of a shrub extract); 5) The study was not exclusively about medicinal uses of the shrub; 6) The study was not a pure modeling
study but rather contained field, laboratory, or greenhouse data in conjunction with the
model; 7) The study was not purely biological or chemical research without regard to
ecology; 8) The study did more than just note the presence or absence of the shrub but
rather mentioned something in regard to the ecology (e.g. densities or regeneration
strategies), uses (e.g. agriculture or carbon sequestration), or management of shrubs; 9)
The article was not a pure review.

Approximately 250 titles and abstracts met the above criteria. The full text of
those manuscripts was reviewed, and that further eliminated nearly 100 manuscripts. For
the final count, approximately 140 articles were included in this review. The studies
could largely be separated into three groups: 1) Those that focus on the landscape
ecology of shrubs (their diversity, densities, growth patterns, carbon storage capacity,
diebacks and increases); 2) Mechanistic studies that study aspects of shrub growth (e.g.
rooting patterns, water usage, phenology, rhizosphere microbiology); 3) Research on
ecosystem services provided by the shrubs (fuel, firewood, soil nutrients, etc.). The
Results section outlines all of the literature on specific shrub species in the WAS. The
Discussion section uses the lens of agroforestry—specifically, the potential of shrubs for
use in climate smart agriculture—to ascertain major themes concerning the landscape
ecology, mechanisms, and ecosystem services of shrubs in the WAS. Both challenges
and benefits of their adoption into agroforestry systems are discussed.

5.4. Results

5.4.1. Overview of shrub studies in the WAS
Of the 64 species searched for in Web of Science, 23 contained fewer than 10 articles per plant. This suggests a large research gap for shrubs in the WAS. Moreover, there were zero references for 3 of the 64 searches. In total, 28 shrubs are found in the literature that meet the criteria for inclusion in this review (Table 5.2). An overwhelming number of articles were excluded because they only researched medicinal and chemical properties of the shrubs. Though not discussed here, it should be noted that most shrubs in the WAS have an enormous medicinal value to local communities and also to pharmaceutical companies.

In total, the results from 120 papers were included in the review. Approximately 20 more articles met the criteria but did not identify specific species and are consequently used for general discussion. Twelve of the 28 shrubs included in this review were from the Combretaceae or Mimosoideae families, and 58 articles referenced G. senegalensis making it the most well-studied species. P. reticulatum was the second-most researched shrub with 36 studies. Combretum micranthum, C. glutinosum, Pterocarpus lucens, and Ziziphus mauritiana each contained over 10 publications, and all the rest had fewer than 10 studies. Most of the shrub research papers were grouped as landscape ecology studies, and after that there was a relatively even split between mechanistic and ecosystem service studies. The following sections cover the literature on the 28 specific shrubs included in this review.

5.4.2. Guiera senegalensis

The first research on G. senegalensis was conducted by Geiger and Manu (1993) who studied the effect of short-range landscape variability on millet growth in the western region of Niger. They described a phenomenon that has been noted in other
studies across the WAS (Wezel et al., 2000). Namely, that eolian sand builds up around the base of shrubs forming micro-topographic highs across a cropped field. These mounds usually form ‘islands of fertility’ with higher levels of soil nutrients, and as a result, crops grow better near shrubs. Geiger and Manu (1993) made three important discoveries: first, that of the 13 dominant plant species in the region, G. senegalensis was predominant; second, that the islands of fertility covered 30% of the landscape and built up around shrubs both because of their low growth habit and because farmers cut back the shrubs and left the branches around the base of the shrubs; and third, that millet yield was 120% greater on the islands of fertility than in the bare zones surround adjacent to them.

Wezel (2000) highlighted that sand deposition around G. senegalensis often occurs in millet fields with high wind erosion. The islands of fertility form from both a redistribution of nutrients by the shrub (i.e., mining nutrients from lower in the profile and depositing them at the surface through leaf drop and surface root turnover) and by trapping nutrient rich dust. G. senegalensis mounds also help with water infiltration, whereas bare zones in between shrubs were subject to high erosion events. Wezel (2000) further measured the topographic highs and found them to be 20 cm high near G. senegalensis. Moreover, he found that the positive shrub effect on millet yield was inversely related to the distance from the base of the shrub extending to 2 m from its base. From 0-1.2 m, millet yields increased by approximately 200%, and from 1.2-2-m the yield increase was around 135%. In addition, Wezel (2000) was the first to study the effect of coppicing (cutting shrubs to the ground) on millet yields. The result was that coppicing reduced competition between shrub and millet. Finally, the paper was the first
to describe shrub densities on millet yield. They found that millet yields could be increased by *G. senegalensis* densities up to 450 shrubs ha$^{-1}$.

Thirteen total studies (including the two mentioned above) report that *G. senegalensis* improved different aspects of soil fertility or that soil nutrient and carbon levels were higher near the shrubs. In two articles, however, the shrub effect on soils nutrients was mixed (positive and negative). Dossa et al. (2008) reported higher levels of P sorption under the canopy of *G. senegalensis* but the effect was reversed when high levels of shrub litter or manure were added to the soil. Dossa et al. (2009) found an overall net increase in inorganic nutrients (N and P) but also that inorganic N was initially immobilized in the first 76 days. Thus, the beneficial shrub effect took time to detect. Interestingly, Gerard et al. (1999), found a highly significant correlation between *G. senegalensis* and millet growth, but the effect was not related to P availability. They concluded that the shrub effect on millet growth was more than just a nutrient effect. Millet yields increased by 68-94% when the branches and leaves of *G. senegalensis* were applied as mulch over the soil surface at the rate of 1000 kg ha$^{-1}$. Dossa et al. (2012) and Bright et al. (Chapter 3 in submission) showed that *G. senegalensis* at high densities (1500 ha$^{-1}$) increased intercropped millet over 12 years by up to 3,000% over millet grown in bare soil. The shrub plots in those studies also increased the growth of groundnuts.

A major theme of the *G. senegalensis* literature is that this shrub is frequently the most dominant woody species in the savanna vegetation of the WAS. In total, 35 articles use the following terminology to describe the distribution of *G. senegalensis* across the landscape: principal, dominant, main species, abundant, very common, or most common.
These 35 studies were conducted in northern, central, and southern Senegal, in western and southwestern Niger, in central, western, and southern Burkina Faso, and in southern Mali. At least two articles were from each country. Allen and Grime (1995) reported that *G. senegalensis* comprised 96% of the woody vegetation in the fallows of Niger with an average density of 848 shrubs ha$^{-1}$. Other authors that describe the dominance of *G. senegalensis* report densities of 240, 310, 451, 477, and 700 shrubs ha$^{-1}$ (Boulain et al., 2009; Gerard, 1999; Hanan & Prince, 1997; Kizito et al., 2006; Lufafa et al., 2008a). Frequently, *G. senegalensis* is the dominant shrub at fallow sites and in the tiger bush forming nearly monospecific stands (Boulain et al., 2009; Brandt et al., 2014; Nicholson et al., 1997; Seghieri & Laloë, 2004). Six papers researched the growth patterns of *G. senegalensis*, either studying their growth patterns in the tiger bush, in fallows, or in patches. Müller (2013) found that *G. senegalensis* was a colonizer species able to rejuvenate quickly and form the tiger bush. Barbier et al. (2010) suggested that the clumping pattern of shrubs into distinct patterns indicates that they have different soil niches. Couteron et al. (1997) studied spatial patterns of *G. senegalensis* in Burkina Faso and also concluded that soil factors, such as depth and surface crusting, promoted shrub clumping patterns. Lufafa et al. (Lufafa et al. 2008a,b, 2009) established that aboveground shrub biomass ranged from 0.44 to 4.58 Mg ha$^{-1}$ which corresponded to aboveground peak season biomass C ranging from 0.9-1.4 Mg ha$^{-1}$. They found that overall mean of soil organic carbon (SOC) to a depth of 40 cm was 17 Mg ha$^{-1}$ (Lufafa et al., 2008b). They concluded that there was significant potential to increase C sequestration by 200-350% over the span of a couple decades if the shrubs were left on the landscape and not burned (Lufafa et al., 2008a).
The morphology, physiology, ecology, and mechanisms that contribute to the dominance of *G. senegalensis* form the backbone of 21 research articles. The results show a plant that is well-suited to the semi-arid conditions of the WAS (Sop & Oldeland, 2013). Many authors describe *G. senegalensis*’s ability to regenerate quickly (Brandt et al., 2017; Gijsbers et al., 1994; Hänke et al., 2016; Vincke et al., 2010). Seghieri et al. (2004) showed that the resprouting ability of *G. senegalensis* enables it to survive coppicing events before crop planting, whereas other woody species lack this ability. Furthermore, the authors described a high degree of physiological plasticity regarding the shrub’s water status. Specifically, *G. senegalensis* was able to thrive even with large spatial and temporal variation in levels of available water. The authors concluded that the ability of *G. senegalensis* to survive a large range of different water statuses was what contributed to its dominance especially after a large disturbance event like drought across the region. Hanan et al. (1997) investigated the ability of *G. senegalensis* to regulate its stomatal conductance ($g_s$) in order to be able to survive in semi-arid conditions and retain its leaves long into the dry season. Brunel et al. (1997) described the extensive surficial root system of the shrub and also that transpiration was only about 20% of total evapotranspiration. The authors also mentioned that rapid infiltration events which are common near the base of *G. senegalensis* (Bromley et al., 1997) makes water available for future shrub use.

Bégué et al. (1994) showed that the diffuse canopy of *G. senegalensis* allows more than 40% of photosynthetically active radiation (PAR) to pass through its canopy, which benefits the growth of crops next to the shrub. Sotelo Montes et al. (2014) and Gaze et al. (1998) reported that the wide distribution of shrub roots of the shrub (deeper
than 4 m and up to 8 m horizontally from the base) allowed them to access water to keep them alive during the dry season. Issofou et al. (Issoufou et al., 2015) described the high soil-to-leaf hydraulic conductance ($K_{s-L}$) in mature and current-year resprouts of *G. senegalensis* which supported the regeneration process. $K_{s-L}$ also increased while $g_s$ decreased. Thus this is the mechanism that shrubs can use to cope with severe seasonal drought and regular disturbance over the long term. Issofou et al. (2013) also described how *G. senegalensis* were able to regulate stomatal closure to regulate transpiration. As long as soil water potential remained $>-3.6$ MPa, the species was able to survive in good condition.

Kizito et al. (2006) described the water ecology of *G. senegalensis*. Soil water content was higher next to shrubs. Also, shrubs used deep water, whereas crops used surface water. Up to 1.10 m depth, the shrubs did not compete with crops for water but preferentially extracted water from the lower portion of the profile below 1.10 m and perhaps beyond 3.5 m. 20% higher soil water storage in the upper 1.10 m of the soil profile compared to sole crop plots. Kizito et al. (2012) established that *G. senegalensis* performed hydraulic lift—the movement of water from wetter zones deep in the soil profile to the soil surface to be leaked into the soil profile out of the roots at night.

Research on soil biology is rare in the WAS. However, 4 studies investigated microbial biomass, microbial community structure (including arbuscular mycorrhiza), and beneficial microorganisms associated with the *G. senegalensis*-millet intercropping system (Diedhiou et al., 2009; Diedhiou-Sall et al., 2013; Debenport et al., 2015; Bright et al. [Chapter 4]). These papers found a significant beneficial effect of the
microorganisms within the rooting zone of *G. senegalensis* on shrub litter decomposition and millet growth.

Four papers described the use of *G. senegalensis* for fodder. Sanon et al. (2007) mentioned that the shrub was the most-frequently browsed woody species by cattle in their study from Burkina Faso and that sheep were also partial to it. Powell et al. (1994) reported that sheep in Niger fed on *G. senegalensis* and that those animals would provide 45-53 kg N and 5.1-7.8 kg P ha\(^{-1}\) annually from a shrub-based diet through urine and manure. This is important because millet in the region requires 36 kg N and 6.1 kg P ha\(^{-1}\). Thus, the authors concluded that animals should be managed using woody vegetation to increase the nutrient balance on cropped fields. There is ambiguity in the literature, however, on how useful *G. senegalensis* is as a fodder source. Brandt et al. (2017) noted that it was “poorly-palatable,” and Wezel and Boecker (1998) concurred. Dossa et al. (2012) suggested that the shrub’s relative unpalatability was an asset for its use in agroforestry systems because shrub residues could be used for mulch without being eaten. In addition to fodder and medicine, *G. senegalensis* is also useful to denizens of the WAS for fuelwood, food, and construction (Sop & Oldeland, 2013; Sotelo Montes et al., 2014; Stoate et al., 2001).

Though the literature on *G. senegalensis* is overwhelmingly positive regarding its usefulness to communities for agroforestry in the WAS, six studies suggest potential drawbacks that might limit their effectiveness. Villagers in southern Senegal recognized that millet yields were sometimes higher next to *G. senegalensis*, but they were hesitant to adopt the shrubs in cropping systems because they felt that they would be destroyed by fire during the dry season (Stoate et al., 2001). In addition, the villagers mentioned that
they did not have enough cows to make it worthwhile for them to plant shrubs for use in
dual cropping/livestock systems. The results from those interviews highlight a common
theme in the literature: agroforestry species are only useful if they provide multiple
ecosystem services (e.g. soil nutrients and fodder). Another barrier to adoption was that
the men who cleared the fields for crops considered *G. senegalensis* to be a weed (Stoate
et al., 2001).

Seghieri et al. (2005) and Issoufou et al. (2013) reported that *G. senegalensis* is
susceptible to severe droughts, and Brandt et al. (2017) and Wezel and Lykke (2006)
described diebacks of the species in Senegal followed by fast regeneration of new
sprouts. As previously discussed, the shrub has remarkable morphological and
physiological attributes that enable it to thrive in semi-arid conditions, but it follows that
*G. senegalensis* would not be useful at the northern, dry extremity of the WAS.
However, its usefulness could extend southward into more fertile soils if the climate
moves the ecological zones south. Like many of the shrubs, *G. senegalensis* also is
susceptible to extreme anthropogenic pressure (Vincke et al., 2010). Though, the shrub
thrives under coppicing and tolerates grazing, management is still needed to ensure that
the shrub maintains a healthy growth habit. Finally, Wezel (2000) described competition
between shrubs and crops if the shrubs was not coppiced; Kizito et al. (2006) showed no
significant shrub effect on crop growth; and Dossa et al. (2008, 2009) noted that the
shrub effect on soil fertility is not immediate and further that mulches needed to be used
in high volume to show a beneficial effect.

5.4.3. *Piliostigma reticulatum*
Many of the articles on *P. reticulatum* overlap with those of *G. senegalensis*. The reason is that *P. reticulatum* is also a dominant shrub across the WAS and sometimes grows in stands with *G. senegalensis* (Gijsbers et al., 1994; Wezel & Lykke, 2006; Wezel et al., 2000; Yelemou et al., 2015). However, *P. reticulatum*’s preferred habitat is generally farther to the south of *G. senegalensis* with more rainfall (Kizito et al., 2006; Lufafa et al., 2009; Wezel et al., 2000). Overall, 11 studies referred to *P. reticulatum* as prevalent, main, principal, important, or dominant. In addition, three authors mentioned that the shrub is increasing in Burkina Faso, Niger, and Senegal (Herrmann & Tappan, 2013; Traoré et al., 2012; Wezel & Haigis, 2000). Like *G. senegalensis*, *P. reticulatum* is often found in fallows and on degraded soils where it is classified as a pioneer species (Yelemou et al., 2007, 2015). At a site in Burkina Faso, its canopy covered >5% of the soil surface. Its natural densities, however, are lower than those of *G. senegalensis*: typically 134-288 *P. reticulatum* shrubs ha\(^{-1}\) in central and southern Senegal (Kizito et al., 2006; Lufafa et al., 2008a; Diédhiou, et al., 2008).

More than half of the *P. reticulatum* research (19 articles) measured the shrub effect on soil chemical properties. Sixteen of the papers described an increase in soil nutrients or fertility near the shrub. Wezel et al. (2000), compared soil nutrients next to 5 shrub species: *G. senegalensis*, *C. glutinosum*, *Annona senegalensis*, *Bauhinia rufescens*, and *P. reticulatum*, and found that N enrichment was highest next to *P. reticulatum*. Dossa et al. (2013) and Bright et al. (2017) measured 10 soil nutrients and C in an 11-year experiment that compared millet and groundnut intercropping with *P. reticulatum* at densities of 1000 shrubs ha\(^{-1}\) with cropping in bare soil. They found that the shrub plots were significantly enriched in N, K, Ca, Mg, and S. Furthermore, the authors showed the
significant potential of the *P. reticulatum* intercropping system for soil C sequestration. In addition, millet yields were approximately two times greater in the shrub plots (Bright et al., 2017). The authors concluded that their *P. reticulatum* intercropping system was especially beneficial to farmers in the WAS because groundnut yields with shrubs but no fertilizer were higher than yields receiving 1.5X the recommended fertilizer rate for the region. Thus, fertilizers, which are expensive and rarely are not be needed for yield improvement. Millet yields were also greater near shrubs Geiger and Manu (1993) and Debenport et al. (2015).

Ten studies focused on soil biology or soil hydrology. A handful of them overlapped with the articles on *G. senegalensis* and had similar results (Diedhiou et al., 2009; Diedhiou-Sall, et al. 2013; Debenport et al., 2015; Kizito et al., 2006, 2007, 2012). Diakhaté et al. (2016) found higher soil enzyme activities and differences in microbial community structure near the shrub than in bare soils next to it. Based on results in their study, Chapuis-Lardy et al. (2015) suggested that *P. reticulatum* leaves and stems could be used to kill plant parasitic nematodes. Finally, Hernandez et al. (2015) found higher arbuscular mycorrhizal spore communities near to the shrub, higher microbial biomass, and higher soil enzyme activity. Yelemou et al. (2013) also described greater microbial biomass underneath the shrub canopy.

*P. reticulatum* is very useful to the inhabitants of the WAS for firewood, food, construction materials, and medicine (Yelemou et al., 2007). Four studies described its usefulness as a fodder species, and the seed pods are often fed to animals. However, Wezel and Boecker (1999) mentioned that the leaves were relatively unpalatable and
disliked by animals. Lamers et al. (1995) found the shrub to be useful for windbreaks, and Diack et al. (2000) described its usefulness for mulch.

Seven papers investigated the mechanisms, ecology, and physiology behind the superior growth of *P. reticulatum*. Yelemou et al. (2007, 2015) specified that it was adapted to low rainfall, to degraded soils with low C and high sand, and importantly, that it had a high tolerance for drought. Furthermore, those authors found that the shrub regenerates with little assistance. Gijsbers et al. (1994) concurred with the strong regeneration ability of the shrub, and Sotelo Montes et al. (2014) showed that it grows quickly. *P. reticulatum* also performs hydraulic lift and had the same spatial offset in water use seen with *G. senegalensis* which reduced its competition with crops (Kizito et al., 2012; Kizito et al., 2007). Finally, Bright et al. (2017) found that *P. reticulatum* uses water from the previous rainy season to sustain its growth, and that was part of the reason why the shrub did not compete with crops for limited water.

There were 6 studies that mentioned potential drawbacks of *P. reticulatum* for agroforestry. Barthès et al. (2015) found that a mulching treatment of buried shrub leaves and branches had no effect on soil C, N, P, or sorghum grain yields. The author concluded, however, that this was probably because of the low application rate and because of the spatial heterogeneity. *P. reticulatum* caused N immobilization near its roots in the short term (Iyamuremye, 2000). Dossa et al. (2013) found no significant effect of the shrub on groundnuts, but Bright et al. (2017) did and concluded that the shrub effect took at least 8 years to benefit groundnut yields. Sotelo Montes et al. (2014) described the shrub as not a useful fuelwood species. Finally, the species does appear to be somewhat susceptible to anthropogenic pressure (Yelemou et al. 2015), and Brandt et
al. (2014) also discussed diebacks of the species in Senegal and Mali concluding that it was not very robust to poor soil conditions.

5.4.4. Combretum micranthum

Unlike the two previously-described shrubs which are semi-evergreen (meaning they keep their leaves for most of the year and only lose them at the very end of the dry season), *C. micranthum* is a deciduous shrub and loses its leaves soon after the start of the dry season (Barbier et al., 2008). The search for the species by title yielded 16 articles. However, none of them solely studied *C. micranthum*, though a couple were written about species of the Combretaceae. Though less-researched than *G. senegalensis* or *P. reticulatum*, half of the literature on *C. micranthum* report its dominance in Niger and Burkina Faso. Eight papers describe its distribution with the terms: most abundant, abundant, most frequent, most prevalent, and dominant. In Southwest Niger and Burkina Faso, the density of *C. micranthum* was 1080 and 413 ha\(^{-1}\) respectively (Couteron et al., 2000). At another site in Northwest Burkina Faso, the *C. micranthum* density was 531 ha\(^{-1}\) and comprised 91% of the abundance in the tiger bush (Couteron, 2001). The authors noted that the shrub was dominant in the northern Sahelian zone. It was also typically found in the tiger bush or fallows (Boulain et al., 2009; Müller, 2013). In addition to the 8 articles mentioning its dominance, three articles described either its wide distribution (Wezel & Lykke, 2006) or that it was the second-most prevalent species on the landscape (Boulain et al., 2009; Mahamane & Mahamane, 2005).

Bognounou et al. (2010a,b) found that *C. micranthum* primarily regenerates and spreads by seedlings whereas other shrubs in the Combretaceae (e.g. *C. nigricans* and *C. aculeatum*) spread vegetatively. Furthermore, *C. micranthum* seedlings were well-suited
for restoration of degraded lands (Bognounou et al., 2010a). Barbier et al. (2008, 2010) discussed the clumping patterns of the shrub and concluded that plant-to-plant interactions facilitated their dominance across the landscape. They also noted that soils were more moist underneath the shrub which was similar to the results for *G. senegalensis* and *P. reticulatum*. No articles studied the effect of *C. micranthum* on crops, but one study showed its usefulness as a fodder species for sheep (Sanon et al., 2007). Another study confirmed that it was useful for food and construction (Sop & Oldeland, 2013).

5.4.5. *Combretum glutinosum*

*C. glutinosum* is another prominent shrub in the WAS. Ten studies in northern and southern Senegal, Burkina Faso, Mali, and Niger mention its robustness. Brandt et al. (2014) found that it increased in Senegal and Mali between 1982-2010. In a survey of multiple sites across Senegal, Niger, and Burkina Faso, Wezel and Lykke (2006) noted *C. glutinosum*’s presence at many locations. Though sparse, it was dominant on sand dunes and on sandy soils (Hiernaux et al., 2009). Its density was 72 ha\(^{-1}\) in western Niger (Geiger and Manu, 1993). Like *G. senegalensis*, *C. glutinosum* is also a significant component of the fallows (Manlay et al., 2004; Wezel & Boecker, 1998). Moreover, Herrmann and Tappan (2013) found that it colonized disturbed sites with high anthropogenic pressure. They suggested that the shrub was negative for long-term ecosystem function because it tended to form monospecific stands which choked out diversity. Two authors, however, recorded decreases or diebacks of the shrub in the Ferlo of northern Senegal and in Niger (Berger et al., 1996; Wezel & Haigis, 2000).
Another two authors noted the strong regeneration abilities of the shrub which contributed to its dominance (Gijsbers et al., 1994; Stoate et al., 2001). Gijsbers et al. (1994) found that *C. glutinosum* was suitable for land restoration because it was able to sprout abundantly from rootstocks. Two studies reported increased soil organic matter or nutrients in the rooting zone of the shrub (Stoate et al., 2001; Wezel et al., 2000), and Geiger and Manu (1993) found that millet yields were higher next to the shrub. The shrub provided good fodder for sheep (Powell et al., 1994) and was also suggested as an excellent firewood species (Sotelo Montes et al., 2014). Two studies mentioned its use as firewood (Nygård et al., 2004; Wezel & Haigis, 2000) and for construction and windbreaks (Stoate et al., 2001).

### 5.4.6. *Combretum aculeatum* and *C. nigricans*

To complete the literature review of the Combretaceae, 5 studies mention the growth and distribution of *C. aculeatum* and *C. nigricans*. Bognounou et al. (Bognounou et al., 2010b) found that the former shrub was more prevalent in the Sahelian zone whereas the latter was more abundant in the Sudanian. Hiernaux et al. (2009) described *C. aculeatum*’s prominence on sandy sites. *C. nigricans* was one of 5 dominant species in the tiger bush of southwest Niger (Bromley et al., 1997) and was also abundant at 5 sites in central Burkina Faso (Nygaard et al., 2004). Both species germinated well from seeds and were suitable for plantations that could be used to restore degraded lands (Bognounou et al., 2010b).

### 5.4.7. *Pterocarpus lucens*

*P. lucens* is a member of the Fabaceae (Table 5.1) and fixes nitrogen. Sylla et al. (2002) studied the strains of rhizobia that infect the plant and fix the nitrogen. The
authors found that \textit{P. lucens} fixed less N than other shrubs in the WAS—\textit{Leucaena leucocephala} and \textit{Acacia} spp.—and classified it a low N-fixing shrub (Sylla et al., 1998).

In the tiger bush of Mali and Burkina Faso, several authors found that \textit{P. lucens} was either the most abundant or a principal species (Couteron, 2001; Couteron & Kokou, 1997; Couteron et al., 1996; Hiernaux & Gérard, 1999; Müller, 2013). Sop et al. (2011) counted densities of 108-170 shrubs ha\(^{-1}\) in Burkina Faso and mentioned that the shrub was a stable species (neither experiencing diebacks or increases). Thus, the species has a level of drought tolerance. Couteron (2001) found that \textit{P. lucens} was co-dominant with \textit{C. micranthum} in the northern Sahelian zone of Burkina Faso and recorded a mean density of 65 plants ha\(^{-1}\). The shrub was also dominant on ferruginous soils in the eastern Ferlo zone of northern Senegal which is mostly used for livestock grazing (Brandt et al., 2014). Two studies, however, noted that the shrub had either decreased on sites in Burkina Faso, Niger and Senegal, or was perceived by local inhabitants to be “threatened” (Sop & Oldeland, 2013; Wezel & Lykke, 2006). Moreover, Sop et al. (2011) noted that the species regenerated poorly under field conditions in the Sahelian zone of Burkina Faso. Nevertheless, under greenhouse conditions, Ky-Dembele et al. (2016) researched propagation methods for the shrub and discovered that it was an easy-rooting species suitable for vegetative propagation and landscape restoration efforts.

\textit{P. lucens} is unparalleled as a fodder species. Hamer et al. (2007) said it was the most widely-used fodder tree in the Segou region of northern Mali and that its leaves are highly preferred by livestock. Sop et al. (2011) described it as one of the most desirable woody species in the Sahelian zone of Burkina Faso and that it was especially important for animals in the dry season. \textit{P. lucens} is the preferred browse species for goats (Sanon
et al., 2007). The shrub is intensively harvested for food and construction in Burkina Faso (Sop et al., 2013). Another novel use of *P. lucens* was recorded by Mando et al. (1997a, 1997b; 1999; Mando & Stroosnijder, 1999). They applied *P. lucens*’ mulch to the surface of fields with surface crusting and found that termites ate the mulch and increased soil organic matter in the fields which increased water infiltration and content thereby benefiting vegetation.

5.4.8. Ziziphus mauritiana

*Z. mauritiana* (also known as Ber) is widely distributed from India to Senegal and can be found in all countries of the Sahel (Kalinganire et al., 2008). It is often described as a deciduous tree (losing its leaves in the dry season) but takes on a shrub growth habit. Sop et al. (Sop & Oldeland, 2013) noted that it is well-adapted to semi-arid conditions of the Sahel. Two articles recorded increases and decreases for the species in Niger (Wezel & Haigis, 2000; Wezel & Lykke, 2006), and Berger et al. (Berger et al., 1996) described the relative stability of the species.

For farmers, *Z. mauritiana* is one of the most important fruit-bearing species in the Sahel (Kalinganire et al., 2008; Ræbild et al., 2011) both for food and because it commands a good price in local markets. The fruit pulp is consumed directly or made into juices. Wild varieties in the WAS typically have small fruits, and the species is sensitive to diseases which make it a challenging species for agroforestry adoption in the WAS. However, Raebild et al. (2010) discussed the need for domestication of this species similar to what has been done in Asia. This involves new research into the genetics of wild species, hybridization of improved varieties, and developing grafting and vegetative propagation strategies. Some of this research is currently being done in the
WAS including grafting Asian, high-yielding varieties onto Sahelian rootstocks (Sanou et al., 2014) and using arbuscular mycorrhizal fungal inoculation to improve the growth of new seedlings in nursery soil (Sidibé et al., 2012). Three authors described its usefulness for firewood (Kalinganire et al., 2008; Sotelo Montes et al., 2014; Wezel & Lykke, 2006), and it is planted in live fences to protect crops from animals and also to control erosion (Kalinganire et al., 2008; Ræbild et al., 2011).

5.4.9. *Boscia senegalensis*, and *Maerua crassifolia*

Most of the literature on *B. senegalensis* and *M. crassifolia* describe their distribution across the landscape. Both species are well-adapted to sandy, dry, and degraded soils. *M. crassifolia* is drought-averse and persisted on the landscape when other shrubs died in Mali and western Niger (Hiernaux et al., 2009; Hiernaux & Gérard, 1999). Müller et al. (2013) and Hiernaux et al. (1999) found that *B. seneglaensis* was one of the most frequent and core species of the tiger bush in Burkina Faso, Mali, and Niger. Two authors described increasing *B. senegalensis* densities in the Ferlo region of northern Senegal (Berger et al., 1996; Vincke et al., 2010). Nevertheless, farmers in the WAS perceived the shrub to be threatened, i.e., susceptible to diebacks (Sop & Oldeland, 2013) and other farmers mentioned that both *B. seneglaensis* and *M. crassifolia* had decreased (Wezel and Lykke, 2006). Importantly, *B. senegalensis* was one of five shrubs which O’Connor and Ford (O’Connor & Ford, 2014) proposed for use in the Great Green Wall to protect against land degradation in the northern Sahel. The reason is that the shrub grows fast in arid and semi-arid climates on low-fertility soils but reached sufficient heights to be useful as a windbreak. The shrub could be used for honey
production the authors concluded. *M. crassifolia* has important browse value (Ayantunde et al., 1999).

5.4.10. *Acacia* spp.

The *Acacia* genus consists of 6 shrubs: *A. ataxacantha*, *A. ehrenbergiana*, *A. gourmaensis*, *A. macrostachya*, *A. laeta*, and *A. senegal*. These all fix N, and Traoré et al. (Traoré et al., 2012) found that they were highly suitable for agroforestry and afforestation because they are drought-resistant and can withstand grazing. *A. senegal* and *A. laeta* were singled out as especially useful for soil conservation and restoration of degraded lands (Traoré et al., 2012). Those two shrubs are typically confined to the Sahelian zone whereas *A. gourmaensis* is more prevalent in the Sudanian zone. *A. ataxacantha* and *A. macrostachya* are core species and dominant in the tiger bush in Mali and Niger (Bromley et al., 1997; Hiernaux & Gérard, 1999). In Burkina Faso, *A. macrostachya* was well-adapted to semi-arid conditions (Sop & Oldeland, 2013) and also dominant in southern Senegal (Manlay et al., 2004). Wezel and Lykke (2006) found that *A. ataxacantha* was ubiquitous in Burkina Faso, Mali, and Niger, but also that its densities were decreasing. Couteron (2001) recorded an *A. ataxacantha* density of 56 shrubs ha\(^{-1}\) in northwest Burkina Faso. *A. ehrenbergiana* was the dominant species at one survey site with shallow soils in central Mali (Hiernaux et al., 2009), however Wezel and Lykke (2006) described the species’ decrease in the WAS. Zida et al. (2008) researched *A. machrostachya* regeneration and found that seedlings could not be drought-stressed during seedling establishment. However, the authors also recorded 80-98% shrub survival in the field when seedlings were planted in pots and transferred to the field.
Communities in Burkina Faso, Mali, and Niger successfully restored 2,235 ha of degraded lands by planting 55 woody and herbaceous species across the landscape (Sacande & Berrahmouni, 2016). The villages chose to use *A. senegal* for 30% of the planted woody species, and the primary reason was because it produced gum arabic which is an important secondary income source for farmers with the species on their property. Lamers et al. (1994) studied the use of seven woody species for windbreaks, establishment, and fodder in Niger and found that *A. senegal* produced the most abundant dry matter. It also had the highest protein for animal fodder and established and grew quickly. Goats prefer *A. senegal* for browsing (Sanon et al., 2007). However, Vincke et al. (2010) found that it was very sensitive to grazing, and both Wezel and Lykke (2006) and Berger et al. (1996) described decreases of the shrub in Senegal. *A. senegal* was also not a good species for windbreaks (Michels et al., 1998).

5.4.11. *Bauhinia rufescens*

The results for *B. rufescens* were mixed. The shrub is in the same family as *P. reticulatum*. Three studies recorded yield reductions or competition between millet and *B. rufescens* (Mayus et al., 1997, 1999a, 1999b). Surprisingly, however, Wezel (2000) described its beneficial effect on soil nutrients. The shrub is not strong a strong vegetative propagator (Ky-Dembele et al., 2016), but it does have a fast establishment in the field it is very useful for windbreaks (Lamers et al., 1994, 1995; Michels et al., 1998).

5.4.12. *Anona senegalensis*

Three studies mention this shrub in the WAS. Bayala et al. (2011) found it to be widely distributed in Burkina Faso. It was also used to combat wind erosion and could enrich soil nutrients (Lamers et al., 1995; Wezel et al., 2000).
5.4.13. *Calotropis procera*

Like *A. senegalensis*, *C. procera* is a member of the Apocynaceae. Vincke et al. (2010) described the fact that the shrub increased in Senegal from 1976-1995. They also described it as a pioneer species and one that could withstand anthropogenic pressure.

5.4.14. *Dichrostachys cinerea* and *Leucaena leucocephala*

Both species are members of the Mimosoideae like the Acacia spp. Schulz described *D. cinerea*’s N-fixing ability and Ky-Dembele et al. (2007) found that it regenerated from both seeds and root buds with lots of plantlets.

*L. leucocephala* has a wide distribution across Africa and is generally found in the more humid regions of the WAS. It is well-suited for animal browse and for use as a green manure to increase soil C (Balogun et al., 1998; Bayala et al., 2009; Tschakert et al., 2004). Interestingly, Tilander et al. (1995) recommended that the species not be used for agroforestry in BF because the climate was too dry and consequently the woody species competed with crop roots for nutrients and water.

5.4.15. *Grewia bicolor* and *G. flava*

These two species represent the Tiliaceae shrubs. *G. flava* is one of five shrubs recommended by O’Connor and Ford (2014) for inclusion in the Great Green Wall Initiative. *G. bicolor* is a dominant shrub in Senegal and abundant in the tiger bush of Burkina Faso (Couteron et al., 1996; Couteron & Kokou, 1997; Vincke et al., 2010). However, Wezel and Lykke (2006) found the species to be decreasing in the WAS.

5.16. *Lannea velutina*

Only one study mentions that this was a threatened species in Burkina Faso (Bayala et al., 2011).
5.4.16. *Leptadenia pyrotechnica*

This is another dominant shrub in the WAS. On sandy soils in Mali, *L. pyrotechnica* accounted for the majority of the shrubs and formed almost a pure stand of 63 shrubs ha\(^{-1}\). Lykke et al. (2004) surveyed 5 villages in Burkina Faso about the woody vegetation dynamics (increases and decreases). *L. pyrotechnica* was one of 2 species that was “not declining.”

5.4.17. *Moringa oleifera*

*M. oleifera* is an exotic species, but it has become quite important to the inhabitants of the WAS. Sop et al. (2013) described its stability in dry soils, but also that it was fast growing and abundantly used for food, fuel, construction and medicine. (Etongo et al., 2015) studied the reasons why farmers plant woody species and what species they were planting in Burkina Faso. Villagers described it as the third-most important species planted after mango and cashew trees. Its leaves were used for medicine and sold in local markets, and the leaves could also be made into tea. Furthermore, it was also used as a food condiment.

5.4.18. *Salvadora persica*

This shrub has good browse value and is found in moderate populations across the WAS (Ayantunde et al., 1999). It tolerates dry, sandy soils and can be found on dune complexes in Mauritania (Culmsee, 2002).

5.5. **Discussion**

5.5.1. **Designing the 'perfect' agroforestry species**
If one could design a hypothetical ‘perfect agroforestry species’ for the WAS, the task would be daunting. First, one must consider the climate. Over the past 18 millennia, the region has experienced a range of conditions from tropical to desert (Nicholson, 2001). The twentieth century was marked by 4 severe multi-year droughts with concomitant diebacks of the natural vegetation. Recently, there has been an overall increase in both rainfall woody vegetation, yet interannual variability still characterizes the WAS (Nicholson, 2013). Despite the well-established positive relationship between rainfall and vegetation, this review highlights many articles that describe decreases in woody species’ richness and abundance. For scientists, this is merely an ecological progression, yet for the inhabitants of the WAS, who depend on the woody vegetation to sustain livelihoods, this is a dire predicament.

After considering climate, the designer of the ‘perfect’ agroforestry species must contemplate the soils. Da Costa et al. (2015) described the Sahel as, “one of the poorest and most environmentally degraded areas on earth.” Therefore, not only must an agroforestry species sustain its own growth and not outcompete adjacent crops for limited nutrients but also it must increase fertility for the adjacent crops. Moreover, water limits vegetation in some parts of the WAS while nutrients limit it in other parts (Kessler & Breman, 1991). Thus, a prolific, drought-tolerant species from sandy soils of the northern Sahel might grow very poorly on sandy soils in the southern Sahel even with abundant rainfall. The designer, therefore, must comprehend which characteristics of the woody species would best serve specific niche conditions.

“How does the species grow,” is a simple but profound question which must be considered for any agroforestry species. A common problem with agroforestry trees is
that they grow tall and cast shade, and shade reduces growth for many crops. But even if
the species could increase soil nutrients and not compete for water or light, it might have
a very poor regeneration ability and low densities across the landscape which limit its
agroforestry potential. Woody species can increase yields of adjacent crops by 10,000%
but still only exert control over plants within their rooting zone influence. Density,
therefore, is an extremely important attribute of woody vegetation. Moreover, density is
important because the soils in the WAS blow away. Agroforestry species should prevent
that.

A major theme of the shrub literature is the research on the aggregation patterns
of various species. Put succinctly, most shrubs clump together in patches. *P. lucens* was
one of the few species singled out for its ability not to clump (Couteron & Kokou, 1997).
Here again one must consider density. Kessler and Breman (1991) suggested that for
pastoralists, the benefits of shrubs exceeded the negative effects from competition only
up to 15% surface cover. A variation of this concern was expressed by Lykke et al.
(2004) about potential ‘green deserts’ forming in the WAS. This phenomenon occurs
when the landscape becomes dominated by only one species and the ecosystem suffers
biodiversity loss and a concomitant loss of ecosystem services. Thus, for agroforestry,
one must consider the interaction between woody species and the ecosystem services
provided by different species. In summary, a shrub species could actually be too
successful at colonizing degraded lands.

Perhaps most importantly, the goals and knowledge of farmers and landowners
must factor into the design of agroforestry species. The local inhabitants who live with
shrubs understand the details of agroforestry which are often lost on researchers. For
instance, Lykke et al. (2000) surveyed villagers about their perception of woody species and found that they preferred species without thorns. This little morphological trait might literally be overlooked by a researcher designing agroforestry systems, and consequently the most well-suited species would never be implemented because the researcher failed to consider farmers’ views. Unfortunately, there are relatively few studies in the literature that assess the concerns and needs of farmers for agroforestry species.

Most agricultural systems in the WAS are combined crop and animal husbandry operations. The agroforestry designer must ask, “Will crop lands be used for grazing during the dry season?” The choices of woody vegetation might revolve around the answer. A secondary questions is: what species produce abundant, palatable, nutritious fodder while simultaneously increasing crop growth during the rainy season. A farmer might also choose to keep one section of land in traditional fallows for a number of years to improve soil fertility while cropping another section of land. The fallowed land could be used for grazing, and then returned to cropping. In that scenario, a farmer might decide on species that establish rapidly and have strong regeneration capabilities to withstand animal pressure. The Sahel is often described as a ‘cultural landscape’ (Rasmussen et al., 2001). Including the needs and goals of farmers into the design of agroforestry species is merely a recognition that the culture is as important if not more important than the landscape of the Sahel to the success of agroforestry.

Another theme of agroforestry research in the WAS is that the ancillary ecosystem services of an agroforestry species are frequently more important to farmers than the species’ effect on crops. The value of a woody species, then, is positively related to the number of ecosystem services it provides. This is especially true for shrubs
like *Z. mauritiana* and *A. senegal* which have fruits and products that can be consumed or sold at the market for cash. Gender differences should be considered as well. Stoate et al. (2001) characterized many differences between men and women in the perceived value of certain agroforestry species.

Labor costs present a huge challenge for beneficial agroforestry species. Triennially coppicing events take time and a labor force which some farmers do not have. Moreover, many farmers still use fire to clear land for cropping because it is cheap (in terms of labor costs), quick, and effective (Stoate et al., 2001). Woody saplings used for regeneration efforts need to be protected and watered through the dry season for at least a couple years until they establish (Bayala et al., 2014; Omondi et al., 2016). Issues of land ownership present a conjoined challenge to woody vegetation establishment in the region. If long-term land tenure is not in place, farmers see little benefit for establishing woody species because it typically takes several years for a return on investment (Stoate & Jarju, 2008). It follows, then, that species with a rapid establishment are generally more beneficial. Hamer et al. (2007) found that farmers in the WAS typically implement risk-minimizing survival strategies.

Many stakeholders are involved in efforts to decrease land degradation in the WAS by increasing woody vegetation. Currently, the Royal Botanic Gardens at Kew are engaging in partnerships with local communities to identify and propagate well-adapted native species (Sacande & Berrahmouni, 2016). The government of Burkina Faso, the World Agroforestry Center (ICRAF), the National Seed Centre of Burkina Faso (CNSF) and a plethora of other nonprofits including: SOS Sahel, TREE AID, FRUITEQ, Foods Resource Bank, and African Cashew Initiative are all providing seedlings to farmers for
free or at a discounted price (Etongo et al., 2015). This is because hundreds of tons of seeds are required to restore degraded lands, and/or lots of nursery space for seedling regeneration (Sacande & Berrahmouni, 2016). It would be almost impossible to accomplish this without many stakeholders. Consequently, species that are easily-propagated and distributed would be most beneficial for partnerships with development agencies.

The last major barrier for designing a “perfect” agroforestry species is a twofold challenge. There is both a lack of research on suitable species and very little dissemination of the research results. Hamer et al. (2007) found that the two principal costs for using shrubs in the WAS were labor and obtaining good information about their uses. For this review, we searched for sixty-three shrubs, but only included 27 because there were no relevant studies on the other 36 in the WAS. Only 6 species were studied in 10 or more articles. Sacande et al. (Sacande & Berrahmouni, 2016) discussed the urgent need for extension services in the WAS to integrate farmers’ local knowledge with scientific research. Moreover, those authors mentioned that a lot of agroforestry research was published in the so-called ‘gray’ literature and not fully accessible to local communities.

5.5.2. Shrubs and the future of agroforestry research

Though the question posed in the previous section—“What is a perfect agroforestry species for the WAS?”—cannot be answered and was meant only to emphasize the challenges to agroforestry in the region, the results from this review suggest a large and untapped potential of shrubs for agroforestry in the region. Importantly, the results further suggest that shrubs are better-suited than trees for
preventing land degradation, buffering climate change, and increasing food security by raising crop yields. This is because they have morphological, physiological, and ecological adaptations that make them well-suited for benefiting crop growth, stabilizing soils, and increasing carbon sequestration in the area.

The principal theme emerging from this review was that many shrub species are dominant across the landscape. Indeed, the literature suggests that if trees were not selected by farmers in the parklands, the entire region might be largely covered by shrubs. A potential bias of this review, however, is that the literature search was for specific shrubs, and consequently tree surveys would have been omitted. Nonetheless, at least 25 articles surveyed all woody species in the area, and shrubs were invariably the most dominant component of the vegetation. Many of the studies describe shrub dominance on very marginal or degraded lands. On those lands, the shrubs aggregate and sometimes form monospecific stands. The genetics and causes behind the aggregation are still not well-understood, however. Another research question is whether shrubs could be planted by humans in the bare patches between the tiger bush in order to try and make a homogenous stand across the landscape instead of the typical patterns.

While the shrubs in the tiger bush increase water infiltration and soil nutrients, several authors found that this land use along with fallows used for livestock were seldom used by the inhabitants of the WAS. A major research gap, then, is how the tiger bush and fallows could be incorporated into farming and other strategies to mitigate land degradation, climate change, and increase yields. Moreover, how long does it take for tiger bush and fallow lands to be restored to profitability for crop production, and will
there be an ecological succession away from the tiger bush after a certain number of
years?

Many of the current shrublands were once arable. Nevertheless, overgrazing, climate change, and population density altered the ecosystem. Research by Dossa et al. (2012, 2013) and Bright et al. (2017) suggests that the high natural densities of shrubs in monospecific stands of the tiger bush and fallows could be used by farmers to increase yields and C sequestration on degraded lands. Shrub densities were comparable from the tiger bush literature and the shrub- intercropping experiments. However, it is unclear whether the densities in Dossa et al. (2012, 2013) are ecologically and socioeconomically sustainable at the landscape scale. More participatory farmer research is needed to determine the feasibility of high-density shrub intercropping systems and whether an agroforestry adaptation of the tiger bush is beneficial to farmers. In addition, more long-term research stations are needed that measure the effect of different densities of multiple shrub species on yields and soil quality. Though logistically difficult to establish and maintain, these stations could provide a wealth of important information for extension agents and farmers.

Another area for future research concerns the ecological, morphological, and physiological interactions between multiple woody species. Hernandez et al. (2015) found that *P. reticulatum* was an effective nurse shrub for mango trees. This suggests that other shrub species could be used to foster the growth of more economically-valuable tree species. Future studies should address tree planting within the canopy of shrubs. Furthermore, mixed shrub/tree systems are found throughout the WAS, but (to the best of our knowledge) no research has been done on inter-plant signaling, defense
mechanisms, growth, and common mycorrhizal networks between species. This research is arguably very important for understanding patterns of multispecies shrub growth and establishment across the landscape and how to manage interspecies competition and facilitation. Furthermore, this research could help explain why certain species grow better in certain areas and not in others. The reasons behind this are currently poorly understood.

A further theme of the literature was the strong regeneration and vegetative propagation of shrubs. Their landscape dominance was partly attributed to this characteristic. Yet, vegetative and sexual propagation techniques have only been studied for a handful of species. This important research gap is a weak link for further regional shrub use.

Shrubs almost uniformly increased soil nutrients. Even those few studies that mentioned immobilization or decreases suggested that the trends were short-lived. Nevertheless, only five species were investigated for their effect on crop yields. Most of that research was conducted for *G. senegalensis* and *P. reticulatum*. Those are the two most ubiquitous shrubs in the region and consequently, perhaps the easiest to study. Only one species, *B. rufescens*, showed decreased yields next to the shrubs in multiple studies. Nevertheless, at this time we can only hypothesize that most shrubs increase yields. Future studies should examine this more carefully. Water balance and HL studies by Kizito et al. (2006, 2007, 2012) yielded extraordinary insight into why shrubs and crops don’t compete. Yet, again, it is only conjecture that the same phenomena are true of other shrubs?
An emerging area of research is the shrub rhizosphere biology. The results from *G. senegalensis* and *P. reticulatum* show an increase not only in microbial biomass but also in beneficial microorganisms. It is not understood why that is the case and if it is possible to select and culture certain strains for further yield increases. Though there is little investment in plant breeding in the WAS, results from this review suggest that breeding research should involve crops next to shrubs. For example, could the genetics of shrubs and crops contain keys to help understand why, when, and how crops grow better next to shrubs? Are various genes regulated by microorganisms in the rhizoplane of both shrubs and crops? These are questions that demand more research.

5.6. Conclusions

After examining trees for use in agroforestry systems, Breman and Kessler (1997) concluded that the three main reasons why a species does not benefit farmers are: 1) they only add value in the most resource-poor ecosystems which are already too degraded for crop production; 2) the woody species outcompetes crops for resources; 3) the woody species cannot return enough litter inputs to the soil to build organic matter because either animals overgraze them or they are susceptible to drought. The large body of literature in this review suggests that shrubs counteract those three challenges. First and foremost, they are ubiquitous across the Sahel in parklands and steppes, in forests and savanna, on dunes and rocky outcrops. While the literature suggests that the greatest agroforestry potential of shrubs is for marginal lands, nevertheless, the shrubs are very suitable for use in the parklands, and farmers routinely clear them from fields about to be used for cropping. Furthermore, the literature described a remarkable lack of competition
between shrubs and crops. The mechanisms behind this lack of competition are numerous and varied. Furthermore, the high densities of shrubs and the fact that they produce multiple branches, makes them abundant biomass producers that respond well to grazing pressure. They can simultaneously be used for grazing, and yet they withstand grazing pressure.

The many beneficial attributes of shrubs for agroforestry and the relative lack of studies on their use in shrub intercropping systems suggest that shrubs are underutilized, underappreciated, and understudied. This belies their potential importance to agroecosystem function in the WAS. The results are overwhelmingly positive for the benefits of two shrubs, *G. senegalensis* and *P. reticulatum*. They have multiple uses for firewood, fodder, medicine, construction, food, and to build soil nutrients. Moreover, their regeneration abilities and status as pioneer colonizing species is unparalleled. Though certain authors have described shrub-dominated ecosystems as impoverished, degraded, or deserts, the literature contradicts those assertions. We also conclude that researchers should take more care to correctly distinguish trees from shrubs and not confuse the two. Altogether, many articles lump the two groups together, the literature clearly indicates morphological, physiological, and ecological differences between the two. There are many research gaps for shrub use in agroforestry systems of the Sahel. However, the immediate needs are largely to disseminate shrub technologies to farmers and for use in the Great Green Wall and other land restoration initiatives. While climate change and increasing population density severely threaten ecosystem function in the WAS, research shows that shrubs are well-suited to counterbalance those threats.
5.7. References


of a dominant shrub in Sahelian agrosystems, Guiera senegalensis J. F. Gmel. 


Yamba, B., & Sambo, M. (2012). *La régénération naturelle assistée et la sécurité alimentaire des ménages de 5 terroirs villageois des départements de Kantché et Mirriah (région de Zinder, Niger).* Retrieved from 1246-VU Amsterdam:


Table 5.1. Sixty-four shrubs searched for and number of references found in ISI Web of Science. Species description represents Shrub (S), Tree (T) or both classifications in Arbonnier (2004). * represents an exotic shrub † indicates that the search string contained the shrub name followed by (sahel* OR west africa*)

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*Population must increase rapidly—more rapidly than in former times—and ere long the most valuable of all arts, will be the art of deriving a comfortable subsistence from the smallest area of soil. No community whose every member possesses this art, can ever be the victim of oppression of any of its forms. Such a community will be alike independent of crowned-kings, money-kings, and land-kings.* – Abraham Lincoln

Strategies for strengthening food security in the West African Sahel

The Sahel is one of five regions in the world where food production began (Diamond, 1999). Arguably, however, its agriculture has changed little from the dawn of civilizations until now. Subsistence farming, which relies on manual labor and animal traction without the aid of synthetic inputs, is still the predominant practice. Livestock husbandry is still a pastoralist lifestyle, where herders drive sheep, cattle, and goats through a patchwork of cropped, fallowed, and unused fields searching for food. The average farm size is still 1-5 hectares – essentially the maximum area that can be managed without the aid of mechanized equipment. Pearl millet, which was domesticated in the West African Sahel (WAS) 3,000-5,000 years ago (Jukanti et al., 2016), is still the region’s staple crop.

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1 Address to the Wisconsin State Agricultural Society. September 30, 1859.
For development agencies, policymakers, and governments seeking to strengthen food security in the WAS, there are several responses to its current subsistence-based agriculture. The first is to consider it outmoded and in need of structural overhaul. Those favoring this strategy seek a large-scale investment in mechanized farm equipment\(^1\), synthetic fertilizers, herbicides, and pesticides to be distributed to communities for use by local farmers in a cooperative system. While ambitious, this development goal requires significant international investment. Furthermore, the complication of how, when, and where to distribute machinery and fertilizers coupled with the extreme potential for corruption surrounding their allocation and distribution makes this strategy largely prohibitive, even if the resources were obtainable. Moreover, the lack of infrastructure coupled with the natural limitations of soil, climate, and the savanna vegetation severely limit if not eliminate the possibility of achieving a Green Revolution, like that of the 1960s, in the WAS.

At the opposite end of the spectrum, the second response is simply to retain the status quo—do nothing. The reasoning behind this narrow interpretation of food security is that farmers have successfully cultivated the WAS for millennia, overcoming the vagaries of weather, ecology, technology, and political dynasties. The very fact that farming systems built on millet, cowpea, and groundnut rotations remain foundational in the WAS and produce reliable, if small, yields attests to their resilience. The difficulty

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\(^1\) The author has observed multiple fields filled with rows of tractors at the École Nationale Supérieure d’Agriculture (ENSA) in Thiés, Senegal. These were allegedly bought by the Senegalese government to be distributed to farmers or farming communities (Dr. Ibrahima Diédhiou, personal communication).
with this response is that globalization and climate change have engendered a bevy of novel demands and constraints on the WAS; for example: rapid population growth, increased meat consumption, and unremitting temperature increases. Taken together, these challenges are beyond normal fluctuations and consequently are straining the ecological capacity of the WAS to produce a reliable, adequate food supply.

The third response to increase food security is to focus on new conservation agriculture (CA) techniques such as mulching, green manures, windbreaks, and new planting strategies. These methods effectively increase yields, however, there is a large variability in the magnitude of their responses (Bayala et al., 2012). Moreover, CA systems rely heavily on tradeoffs in opportunity costs which limit their potential for wide-scale adoption. For example, Mason et al. (Mason et al., 2015a) note that crop residues are typically used for animal feed or fuel which limits their use as mulch. Therefore, to reduce the use of crop residues as feed or fuel would require new forage sources (for example, an increase in woody species that are favorable fodder sources) and/or alternative fuel sources which might not be available in the region or are prohibitively expensive for farmers.

The fourth response is to establish cropping systems in tandem with the native, savanna vegetation of the Sahel. An example of this strategy is to intersperse crops with the evergreen shrubs, *Piliostigma reticulatum* and *Guiera senegalensis*, as described in Chapters 2 and 3 of this dissertation. Such systems can be categorized as agroforestry practices and thus an extension of the CA techniques discussed in the previous paragraph. However, these cropping systems share fundamental differences with the parkland agroforestry system that is ubiquitous today in the West African Sahel (WAS). Namely,
the parklands are formed when farmers clear most of the natural savanna vegetation in order to expand crop fields but concurrently retain certain trees for economic benefit (primarily food, fuel, and fodder) not necessarily tied to crop production (Bayala et al., 2014). In contrast, the shrub intercropping systems studied in this dissertation both select for and increase the densities of the savanna vegetation (typically cleared and burned by farmers) in order to benefit crop production. Moreover, parkland trees frequently do not increase crop yields and in fact, sometimes lower them (Bayala et al., 2012). Their value is derived from their ability to supplement farmers’ incomes either directly or indirectly (Sinare & Gordon, 2015). On the other hand, the primary benefit of shrubs is their ability to increase yields, soil fertility, carbon sequestration, and to buffer crops against climate change. In summary, the foundation of the parkland system are tree species with intrinsic economic profitability, whereas the foundation of the shrub intercropping systems are species with high ecological resilience leading to sustainable yields and economic profitability. This development of native shrub intercropping systems is an ecological paradigm shift away from the parkland system.

The methods detailed above are by no means an exhaustive list of strategies to strengthen food security in the Sahel. There is also the potential for overlapping many of these systems. For example, a modified combination of parkland agroforestry that employs trees and shrubs in farmers’ fields might be an ideal coupling of CA practices. In addition, the application of synthetic fertilizer was shown to increase millet yields in both the *P. reticulatum* and *G. senegalensis* intercropping systems (Chapters 2 and 3). This suggests that limited fertilizer use combined with shrub management would help crop production. Furthermore, recognition of the farmers’ deep insight into site-specific
conditions, e.g., which woody species benefit crops and which do not, as well as which labor strategies are reasonable and which are not is imperative to bolster food security. In certain situations, this might even call for a retention of practices that appear antiquated to those unfamiliar with the constraints of the system. Accordingly, sustainable increases in food security will indubitably arise from balancing immediate economic needs with long-term ecological sustainability.

*Subsistence farming and shrub-intercropping systems for increasing food security*

Strengthening food security in the WAS by means of subsistence farming without extensive use of machines or inorganic fertilizers is fraught with challenges, yet there are also significant benefits. The first is that many small-scale farms can adapt to extreme weather events (rainfall, temperatures, or drought) and pest epidemics more easily than a system built on monocultures covering many acres. The biblical analogy follows that a cord of many small strands is much harder to break than a large cord made of one strand\(^2\).

Evidence for the inherent ecological resilience of the many small farms in the WAS is supported by the fact that agriculture has persisted in the region despite drastic climate fluctuations over the last eighteen millennia (Nicholson, 2001). Conditions have ranged from desert to tropical with all gradations in between, yet, as previously mentioned, pearl millet has been and continues to be successfully cultivated by local farmers.

The reliance of farmers on pearl millet production is another inherent benefit of the small-scale, subsistence farming in the WAS. Currently, pearl millet ranks as the

\(^2\) Ecclesiastes 4:12
sixth most-important cereal crop in the world, and 45% of the total global production comes from the WAS (Mason et al., 2015b). Though millet has received very little research investment in breeding high-yielding cultivars, nevertheless, it is highly adapted to drought and high temperatures. Moreover, it will produce crops on marginal soils that are unsuitable for other cereals with higher fertility demands. It can also withstand pests and diseases better than most cereals, and finally, it has a high nutritional value: fiber, proteins, minerals, vitamins, antioxidants, and carbohydrates (Jukanti et al., 2016).

Changing dietary preferences which have accelerated the shift away from millet (which is produced in the WAS and does not require high soil fertility) towards diets based on rice (which is not primarily produced in the WAS and does require higher fertility) should be viewed as a threat to regional food security. Though millet yields in the WAS are typically low, the eminent suitability of this crop for the region suggests that there should be a renewed investment in strengthening millet production systems both through crop management and breeding new varieties.

Chapters 2 and 3 report drastic yield improvements attributable to *P. reticulatum* and *G. senegalensis* management systems that plant the crop next to shrubs and then return shrub residues to the soil surface. Consequently, adopting these systems on more small-scale farms could potentially do a great deal to strengthen food security. In addition, novel breeding programs could be initiated that select varieties which respond to native shrub intercropping rather than the traditional breeding system which selects for varieties that respond to high soil fertility. On the socioeconomic-development side of millet production, emphasis should be placed on opening up new international markets.
for millet grown in the WAS. Food trends in the United States suggest that there could be a growing market demand in the West for this staple crop (Zuckerman, 2014).

Another strength of Sahelian agriculture is the ability to adjust, implement, and quickly adopt new CA practices that increase agroecosystem function. Most of the modern epicenters of farming (China, United States, Canada, Brazil, Argentina, Russia, Ukraine, India, Australia) employ economies of scale to produce massive quantities of food. Efficiency is related to size. These agricultural systems are entrenched and inflexible to rapid change. This characteristic is also true of the socioeconomics and politics responsible for their continued existence. In contrast, implementation of shrub-based intercropping systems in the WAS could be tailored to the individual constraints of a single farmer’s field. For example, if one shrub species grows better in one section of the field and another species is predominant in another section, the system could be optimized to include both shrubs. Subsistence farming can adopt multiple CA techniques to suit the demands of a pastoral and crop production system. Ultimately, the techniques employed by a farmer can be adapted not only to site-specific requirements, but also to intra-season weather conditions. Agricultural efficiency in the WAS, therefore, is related to flexibility and adaptability.

There is an enormous ecological price tag that accompanies agricultural economies of scale: eutrophication, greenhouse gas emissions, biodiversity loss, herbicide-resistant weeds, soil erosion, and groundwater depletion among them. Though the WAS faces environmental pollution, the scale of the degradation is significantly less in subsistence-based agriculture. Unlike industrial agricultural systems, the region has more implementable solutions to simultaneously mitigate environmental damage and

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increase yields. As discussed in Chapter 4, (section 4.2, p. 144) farming in the WAS is primarily a de facto organic system, and consequently the environmental challenges facing the region are different from those in industrial systems. For example, wind erosion is an extreme problem in the WAS, yet shrubs have significant potential to reduce this phenomenon. The burning of woody savanna vegetation still accounts for a large proportion of total greenhouse gas emissions from the agricultural sector: 24 and 32% of the total in Mali and Senegal respectively for a combined total of 10.6 million Mg in CO₂ equivalents (FAOSTAT, 2017). Though the reasons for the continued burning are complicated and location-specific, much of it stems from land clearing for crop and livestock production. Population growth and climate change will increase the pressure to clear more land. Using the predominant savanna vegetation—shrubs—for intercropping systems that can reduce carbon footprints while increasing yields is urgent.

Agricultural scientists recognize three eras in the domestication of crops: the mechanical era from pre-historic times to the late 19th century; the chemical era from roughly 1890 to the end of the 20th century; and the biological era from the turn of the 21st century until the present (Dick & Culman, 2016). The research paradigm of our era emphasizes the biology of agroecosystems in order to develop strategies and technologies that enhance the interactions among microorganisms, plants, soils, and animals which benefit crop yields. The focus on biology is a response to the environmental degradation associated with industrial agriculture and shows that truly sustainable systems closely mimic natural systems. Subsistence farming systems in the WAS are well-suited for researching and for implementing biological technologies that can increase crop growth. In fact, limited access to chemical fertilizers demands a biological systems’ approach to
farming. Research in Chapter 3 shows that it is impossible to achieve a millet crop in the absence of organic amendments to the soil. Chapter 4 shows that arbuscular mycorrhizal fungi (AMF) heavily colonize the roots of millet, and there is a high density of spores in the soil which suggests the importance of this beneficial symbiosis to plant growth in the region. Nevertheless, Chapter 5 describes the dearth of soil biology research for shrub-intercropping systems. It is imperative, therefore, that more research be conducted to understand biological interactions between shrubs and crops and to develop microbial inoculants to enhance growth. This type of research could also encourage the start-up of small companies dedicated to the development of biological technologies for agriculture. Chapter 5 also discusses the need for nurseries to propagate shrubs for land restoration in the WAS. The abundance of small-scale farms would be customers for small-scale, local businesses developing biological technologies. These businesses would not be as dependent on economies of scale to turn a profit as are large fertilizer companies.

The global context of shrub intercropping research

Several salient attributes of the WAS make research on shrub-intercropping systems important for increasing global food security and combatting climate change. The first vital characteristic of the region which makes it globally significant is its size. Spanning approximately 3 million km$^2$ (Le Houerou, 1989), the Sahel is a considerable land resource with the potential for substantial yield gains and carbon sequestration to benefit the planet. Over the past ten years, millet yields from sandy soils without fertilizer or other organic amendments were highly variable across the WAS—between 100 and 2500 kg ha$^{-1}$ (Abdou et al., 2016; Bright et al., 2017; Dossa et al., 2012, 2013;
Hiernaux et al., 2009; Ibrahim et al., 2015; Suzuki et al., 2016; Trail et al., 2016). Nevertheless, a key outcome of the long-term research described in Chapters 2 and 3 is that *P. reticulatum* and *G. senegalensis* intercropping systems can maintain yields through high and low-rainfall years on marginal soils. Though yields in this dissertation were not the highest recorded in the region, they were nonetheless stable, and the evidence suggests that they could increase even more next to shrubs. Consequently, if shrub-intercropping systems could be established on more degraded soils across the WAS, this has the potential to increase greatly total crop production and global food security.

Furthermore, there were 2,000 and 4,000 kg ha\(^{-1}\) more soil carbon in the *P. reticulatum* and *G. senegalensis* intercropping systems respectively than in adjacent bare soils (Chapters 2 and 3). These measurements were only taken from the top 10 cm. Lufafa et al. (2008a, 2008b) showed that there is a large carbon sequestration potential in the aboveground biomass of *G. senegalensis* and *P. reticulatum*. In addition, they concluded that non-thermal management of shrubs over 50 years could increase sequestration by >200%. This suggests that if shrubs are retained in the WAS, or their densities even increased for optimal cropping instead of being burned to clear fields, they could significantly reduce the global carbon footprint while also boosting yields. Such ‘win-win’ ecological outcomes are rare in nature. Therefore, the size of the WAS means that there is a large potential for multiplying the beneficial yield and carbon sequestration effect of these shrub systems across the region.
Forty percent of earth’s land surface is composed of drylands: either arid (12%), semi-arid (18%), or dry sub-humid (10%) bioclimatic zones (Le Houerou, 1996), and approximately 44% of all farmed lands are in the drylands. These drylands are home to approximately two billion people including 40% of the total population of Africa and Asia (United Nations, 2011). Startlingly, the extent of the drylands is only expected to increase throughout the 21st century largely due to climate change (Feng & Fu, 2013).

The conclusions of this dissertation, therefore, could be useful in guiding cropping research in other dryland areas of the world in order to increase global food security. One such outcome would be to increase millet production in other arid and semi-arid lands and increase research on systems that optimize millet growth without the use of chemical fertilizers. As discussed in a previous section, this crop is well-suited to the stresses of increasing aridity and climate change.

Another important conclusion of this research is the potential of shrubs and other woody vegetation to restore degraded soils. Land degradation affects up to 70% of dryland soils (Helldén & Tottrup, 2008) and is a huge financial burden to developing countries, costing them 4-8% of their nation gross domestic product (GDP)(United Nations, 2011). However, the development of agroforestry intercropping systems that rely on the use of local woody species (such as shrubs in the WAS) could be used to combat this challenge. Zomer et al. (Zomer et al., 2016) reported that 43% of all agricultural land globally had at least 10% tree cover. In sub-Saharan Africa alone, >1.9 million km² (47% of agricultural land) has a tree cover >10% (Ilstedt et al., 2016), and

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3 The precipitation/potential evapotranspiration ratio (P/PET) in the drylands is between 0.05 and 0.65.
the World Bank estimates that 1.2 billion people around the world depend on agroforestry systems. Furthermore, shrublands are steadily increasing around the globe from increasing aridity and overgrazing. Allington and Valone (2010) estimate that current changes from grassland to shrubland are occurring on over one quarter of the earth’s land surface. Nevertheless, Chapters 2 and 3 show that the increasing density of shrubs benefit crop growth. Chapter 5 indicates that there is a possibility for the use of many different species of shrubs for intercropping in the WAS, but most of them have not been studied for this purpose because they do not have ‘perceived economic value.’ The same phenomenon might be true in other dryland regions of the world. Consequently, this dissertation suggests that long-term research should be conducted on other agroforestry systems in the rest of Africa specifically, but also across the globe.

Finally, the shrub-intercropping research in the WAS reinforces the conclusion that Green Revolution technologies are not a silver bullet which can be used to increase food security in all parts of the world. To the contrary, continuous cropping without P. reticulatum shrubs or the use of shrub mulch decreased soil carbon even though fertilizers were applied (Chapter 2). Thus, unlike many soils in the world with higher intrinsic fertility, those in the WAS must be managed as an agroecosystem that considers the interactions between chemical, physical, and biological properties. Although this type of management can incur large labor costs, the research in this dissertation reminds us that long-term sustainable yields are possible using local, abundant, and free resources, like shrubs in the WAS, to form crop production systems that enhance yields. These systems, therefore, are not inherently inferior but rather are necessary for achieving food security around the globe.
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correlation or regression analysis. In this study, we used a multiple linear regression model to examine the relationship between crop residue use and socio-economic factors. The model included variables such as per capita income, access to credit, and land tenure security. The results showed that crop residue use was positively correlated with per capita income and access to credit, but negatively correlated with land tenure security. The model explained 45% of the variance in crop residue use.


