Global Change Effects on *Vitellaria paradoxa* (C.F.Gaertn.) and *Cenchrus pedicellatus* (Trin.)

Dissertation

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Dedication

Dedicated to the two most important women, my mum Margaret Tom-Dery and my lovely wife Nana Yaa A. Tom-Dery

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Preliminary remarks

This thesis is based on manuscripts either published (3), under review (1) or submitted (1) to peer-reviewed journals and are referred to in the text by their chapter Arabic numbers as shown below. For consistency throughout this thesis, the figures, tables, sections and sub-sections of all manuscripts were renumbered and all references were summarized at the end of the thesis.

Chapter 2: **Tom-Dery D**, Eller F, Reisdorff C, Jensen K (2017) Shea (*Vitellaria paradoxa* C. F.Gaertn.) at the crossroads: current knowledge and research gaps. Agroforestry Systems 92 (5):1353-1371. doi: 10.1007/s10457-017-0080-y

Chapter 3: **Tom-Dery D**, Eller F, Jensen K, Reisdorff C (2018) Effects of elevated carbon dioxide and climate change on biomass and nutritive value of Kyasuwa (*Cenchrus pedicellatus* Trin.). Journal of Applied Botany and Food Quality 91:88–95. doi:10.5073/JABFQ.2018.091.012

Chapter 4: **Tom-Dery D**, Eller F, Fromm J, Jensen K, Reisdorff C (2018) Elevated CO_2 does not offset effects of competition and drought on growth of shea (*Vitellaria paradoxa* C.F. Gaertn.) seedlings. Agroforestry System doi: 10.1007/s10457-018-0286-7

Chapter 5: **Tom-Dery D**, Jensen K, Reisdorff C (Manuscript submitted to Forest, Trees and Livelihood) Excellent Shea (*Vitellaria paradoxa* C.F.Gaertn.) seedlings recovery after fire: gas-exchange, growth and biomass partitioning assessment.

Box 1: **Tom-Dery D**, Jensen K, Reisdorff C (Manuscript under review for Trees) Allocation patterns of carbon and nitrogen in Shea (*Vitellaria paradoxa* C.F.Gaertn.) after simulated late burning.

Summary

Parklands are important refugia of economic species like shea (*Vitellaria paradoxa*), but are also inhabited by several grass species like kyasuwa (*Cenchrus pedicellatus*) and even food crops making them vital for economic, social and environmental (climate change mitigation) benefits. The inter-play of grasses and trees in savanna ecosystems make them one of the most vulnerable biome to global change. This thesis addresses the effects of several global change factors (CO_2, water availability, fire and or grass competition) on shea and kyasuwa photosynthesis, growth, biomass allocation and nutritive value. The general hypothesis of this thesis is that global change factors interact to produce plant-trait responses in shea and kyasuwa.

The thesis is structured in 6 chapters and two boxes. It includes a general introduction to the topic (Chapter 1), a review manuscript of the multi-purpose tree shea (Chapter 2), four manuscripts as the main part (Chapters 3 – 5 and box 1), and a synthesis discussing the links between the single chapters, their implications, and resulting future research perspectives (Chapter 6 and box 2).

Chapter 2 reviewed literature on shea concluding that a consistent methodology for determining the distribution, density, chemical and nutritional composition as well as characterization of regional populations was required. It also suggested research on eco-physiology of shea seedlings under current and projected climate scenarios and dendrochronology as a tool to determine shea age.

Chapter 3 focused on the effects of elevated CO_2, differences in water availability and in N-nutrition on C4 grass kyasuwa. The findings suggest that elevated CO_2 will make kyasuwa attractive as forage and also result in a change in biomass allocation towards a lower root to shoot ratio (R:S), that ultimately may be harmful for the species especially under dry conditions and low nutrient availability making it less competitive.

Chapter 4 presents findings of the effect of elevated CO_2 on shea seedling as modulated by water availability and grass competition. The findings suggest that elevated CO_2 caused an increase in photosynthetic carbon uptake while the stomatal conductance was reduced resulting in increased carbon uptake per transpired water. However, this was only manifested in higher allocation to stems but no change in biomass. Conversely, grass competition caused a decrease in photosynthesis, growth and biomass allocation.

Chapter 5 described the recovery abilities of shea after fire. Shea seedlings showed exceptional recovery to gas exchange parameters, growth and biomass allocation patterns four months after fire with similar photosynthetic rates, growth and biomass accumulation rates of control and fire treatments.

Box 1 focused on the allocation patterns of carbon and nitrogen in shea seedling leaves and roots after fire. The fluorescence parameters, the nitrogen balance index and $\delta^{13}C$ (leaves and roots) were comparable in the two treatments. However higher N per chlorophyll and C/N ratios were recorded in both leaves and roots in post-fire regrowths. We also recorded significant differences in $\delta^{13}C$ in leaves and roots of shea in both treatments.

Box 2 assessed the presence of growth rings in shea from different ecosystems in Ghana and discussed the potential uses of growth rings in shea research.

In conclusion this thesis suggests future global change (especially eCO_2) looks unfavorable for kyasuwa growth making it less competitive with a reduced nutritive value in drought prone and infertile soils. However, shea growth and adaptation to the savanna ecosystem is promising under future global change.

Zusammenfassung

Savannen-Ökosysteme sind oft von Gräsern wie Kyasuwa (*Cenchrus pedicellatus*) dominiert, stellen aber auch wichtige Refugien für ökonomisch relevante Arten wie Shea (*Vitellaria paradoxa*) dar und werden für den Anbau von Food Crops genutzt. Somit haben diese Ökosysteme eine große sozioökonomische Bedeutung. Wechselwirkungen zwischen Gräsern und Bäumen bewirken, dass Savannen-Ökosysteme eine große Empfindlichkeit gegenüber Faktoren des Globalen Wandels aufweisen. Diese Arbeit befasst sich mit dem Einfluss einiger Faktoren des Globalen Wandels (erhöhte atmosphärische CO_2 Konzentrationen (eCO_2), verringerte Wasserverfügbarkeit, Feuer and Konkurrenz zu Gräsern) auf Photosynthese, Wachstum, Biomasse-Allokation und Nährstoffgehalt von Shea und Kyasuwa. Die grundlegende Hypothese dieser Arbeit ist, dass diese Pflanzeneigenschaften durch Interaktion der Faktoren des Globalen Wandels beeinflusst werden.

Diese Arbeit umfasst 6 Kapitel und 2 Boxen. Sie beinhaltet eine Allgemeine Einleitung (Kapitel 1), ein Review-Manuskript zu Shea (Kapitel 2), vier Manuskripte als Hauptteil (Kapitel 3-5 und Box 1) sowie eine Synthese, welche die Zusammenhänge der verschiedenen Kapitel diskutiert, deren Implikationen aufzeigt und eine Ausblick auf zukünftige Forschung zum Thema gibt (Kapitel 6 und Box 2).

Kapitel 2 befasst sich mit der verfügbaren Literatur zu Shea und schlussfolgert, dass eine einheitliche Methodik zur Bestimmung der Verbreitung, Dichte, der biochemischen Zusammensetzung und der Charakterisierung regionaler Populationen notwendig ist. Darüber hinaus empfiehlt es, Forschung zur Ökophysiologie von Shea-Keimlingen zur Erfassung möglicher Effekte des Klimawandels durchzuführen und Dendrochronologie als mögliche Methode zu Altersbestimmung von Shea zu prüfen.

Kapitel 3 befasst sich mit den Effekten von eCO_2, Wasser- und Nährstoffverfügbarkeit auf das C4-Gras Kyasuwa. Die Ergebnisse deuten darauf hin, dass eCO_2 Kyasuwa als Futterpflanze hochwertiger macht und eine Verschiebung in der Biomasse-Allokation zu einem niedrigerem Wurzel-zu-Spross-Verhältnis (R:S) bewirkt, was zu einer geringeren Konkurrenzstärke unter Trockenheit und Nährstoffmangel führen könnte.

Kapitel 4 stellt Ergebnisse einer Studie dar, welche den Effekt von eCO_2 auf Shea in Abhängigkeit von Wasserverfügbarkeit und Konkurrenz (durch Gräser) untersucht. Die Ergebnisse deuten auf eine erhöhte photosynthetische Kohlenstoffaufnahme hin, während die stomatäre Leitfähigkeit reduziert war, was zu einer erhöhten Wassernutzungs-Effizienz führt. Die erhöhte Kohlenstoffaufnahme manifestierte sich allerdings nur in einer erhöhten Spross-Biomasseallokation, nicht aber in veränderte Biomasse per se. Konkurrenz zu Gräsern führte zu geringerer Photosynhtese und Wachstum.

Kapitel 5 beschreibt die Regenerationsfähigkeit von Shea nach Feuer. Shea-Keimlinge zeigten eine schnelle Regeneration hinsichtlich Gaswechsel, Wachstum und Biomasseallokation. Vier Monate nach einem Feuerereignis waren Photosynthese- und Wachstumsraten ähnlich zwischen Kontroll- und Feuertreatments.

Box 1 befasst sich mit den Allokationsmustern von Kohlenstoff und Stickstoff in Blättern und Wurzeln von Shea-Keimlingen nach einem Feuerereignis. Fluoreszenzparamenter, der sog. Nitrogen-Balance-Index und del^{13}C (Blätter und Wurzlen) waren ähnlich in beiden Treatments. Dem gegenübar wurden höhere Stickstoff-zu-Chlorophyll- und Kohlenstoff-zu-Stickstoff-Verhältnisse sowohl in Blättern als auch in Wurzeln in regenerierenden Keimlingen erfasst. Außerdem wurden signifikante Unterschiede in del^{13}C zwischen Blättern und Wurzeln von Shea beider Treatments erfasst.

Box 2 untersucht die Ausprägung von Jahresringen in Shea verschiedener Ökosysteme in Ghana und diskutiert die mögliche Forschungsanwendung.

Zusammenfassend deutet diese Arbeit darauf hin, dass sich der Globale Wandel (speziell eCO_2) negativ auf das Wachstum von Kyasuwa auswirkt. Der Globale Wandel reduziert die Konkurrenzstärke und den Nährstoffgehalt von Kyasuwa in trockheitsanfälligen und unfruchtbaren Böden. Im Gegensatz dazu erscheint das Wachstum und die Anpassung von Shea an Faktoren des Globalen Wandels vielversprechend.

CHAPTER ONE

1 GLOBAL CHANGE IN SAVANNA ECOSYSTEMS -AN INTRODUCTION

1.1 Savanna ecosystems

Savanna ecosystems are characterized by the co-dominance of two different plant life forms – trees and grasses (Scholes and Archer 1997; Sankaran et al. 2004; Shorrocks 2007). Savannas constitute one of the largest biomes of the world, covering about 20 % of the world's land surface and are responsible for 30% of the Earth's terrestrial primary production and also playing a central role in global carbon budgets (Grace et al. 2006). The majority of savanna biomes occur in Africa, with smaller extents in South America, India, and Australia (Fig. 1.1). The savanna biome is the most widespread biome in Africa; extending from the West Coast to East Africa and then round to Angola and Namibia sandwiched between rain forest and desert (Scholes and Archer 1997; Shorrocks 2007).

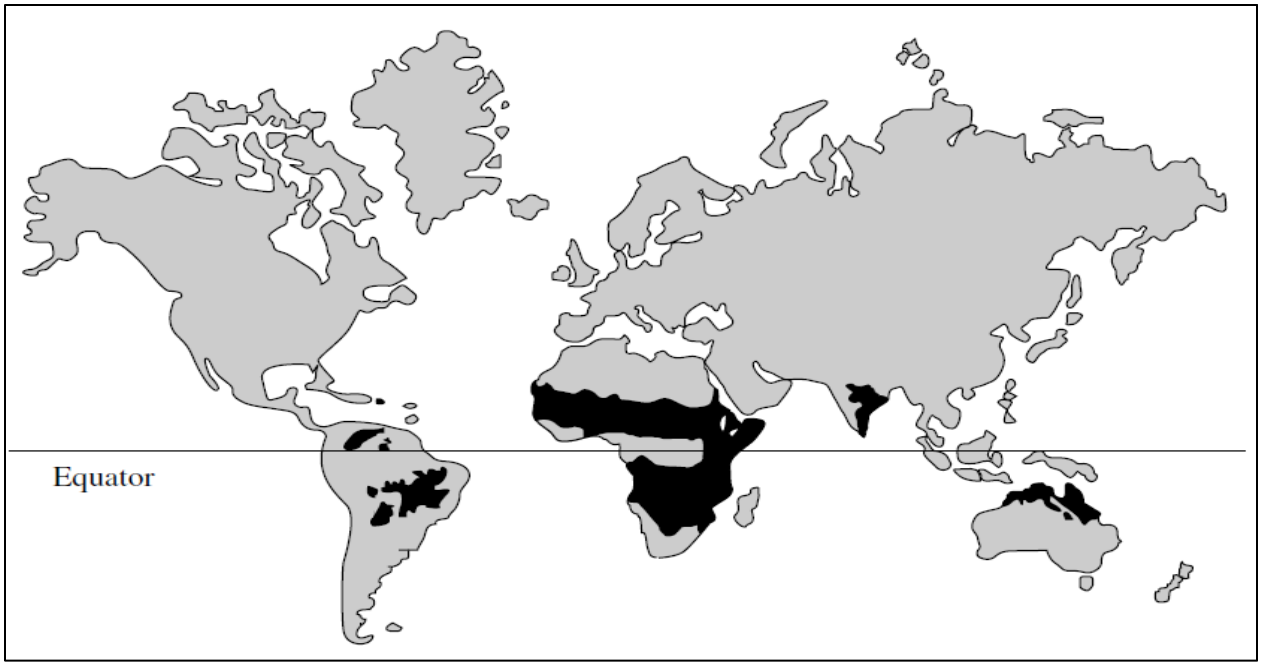

Figure 1.1 World distribution of the savanna biome (Shorrocks 2007)

Savannas are globally important ecosystems of great significance to human economies (Sankaran et al. 2005), because they support a large proportion of the world’s human population and most of its wild herbivore biomass, livestock and rangeland (Scholes and Archer 1997). Temperature and rainfall are major determinants of savannas world-wide except in Africa where temperature variations are relatively small (Shorrocks 2007). Granting that the dominant factor controlling the potential amount of woody cover in savanna ecosystems is precipitation, actual woody cover is controlled by landscape disturbance, much of which is attributable to fire (Bond 2005; Sankaran et al. 2005). The dominant grasses in savannas tend to be C4 grasses with C3 grass species only in some very wet environments (Shorrocks 2007; Bond 2008).

Savannas in African have been classified based on their climatic and edaphic ranges, their physiognomy and structure, or the functional attributes of the dominant life-forms which are not always mutually exclusive and often used interchangeably (Sankaran and Ratnam 2013). Based on the presence or absence of woody species, the savanna is divided into the savanna woodlands, tree and shrub savanna and the grass and shrub savannas (Shorrocks 2007; Sankaran and Ratnam 2013). Agroforestry parklands are generally a tree and shrub savanna type.

1.1.1 Agroforestry parklands

Agroforestry parklands are generally defined as savanna landscapes in which mature trees occur scattered in cultivated or recently fallowed fields (Pullan 1974; Bonkoungou et al. 1994; Boffa 1999a). The process of parklands formation is dependent on traditional agricultural practices such as selective clearing of natural vegetation leaving only preferred woody species on the land when establishing crop fields (Nikiema 2005). Unlike other savanna ecosystems that evolved under the influence of natural processes, parklands mirror deliberate anthropogenic manipulation of trees in agricultural production systems (Boffa 1999a). However, the physiognomy of parklands are comparable to ‘tree savannas’ and have been referred to as such (Boffa 1999a). Parklands are now regarded as the most widespread farming system in the Sahelian zone (Bayala et al. 2015). They are multi-purpose systems that provide, in addition to cereals, tree products such as vegetables, fruits, vegetable oil, firewood, fodder, and medicines and as such are composed of mostly fruit trees (Nikiema 2005). Common species recorded in the parklands are *Vitellaria paradoxa* (shea), *Balanites aegyptiaca, Sclerocarya birrea, Bombax costatum, Lannea microcarpa, Sterculia setigera,* and *Parkia biglobosa* (Pullan 1974; Boffa 1999b; Nikiema 2005). The agroforestry parkland systems have been described as good examples of traditional land use systems and management practices for biodiversity (Boffa 1999b; Schreckenberg 1999; Lovett and Haq 2000).

Figure 1.2 Various shea parklands in Ghana

1.2 Global change effects on savanna ecosystem

The term ‘global change’ is used to describe changes in climate and land use of the planet threatening both biodiversity and traditional land use systems (Walker et al. 1999). One of the foremost foci of ecological research in savannas during the last decades has been understanding how global change translates into shifts in species composition, vegetation structure and biogeochemical cycling over space and time (Oliveras and Malhi 2016). Research on global change is largely multifaceted and attempts to understand how drivers of change impacts socio-ecological systems across different scales going from the level of organisms to the whole earth system components (Camill 2010). Global climate change implies predicting the movement of ecotones (Weltzin and McPherson 2000) which in the Tropics infers savanna areas extending to forest or getting invaded by trees depending on several interacting factors such as atmospheric CO_2 concentration, afforestation, changes in fire regimes, herbivore pressure, and water availability (Parr et al. 2014). Savanna ecosystems are believed to be amongst the most sensitive biomes to future climate change (Sala 2000; Bond et al. 2003).

1.2.1 Effect of elevated CO_2 on savanna grasses (C4) and trees (C3)

Atmospheric CO_2 concentration has more than doubled since the last glacial maximum (LGM) and might double again within this century, largely because of anthropogenic activity (Hartmann et al. 2013; IPCC 2014). Plants responses to increased eCO_2 are generally dependent on their photosynthetic pathways. Agroforestry parklands are mainly inhabited by economic trees like shea which are C3 plants and crops (*Zea Mays*, *Pennisetum glaucum*, *Arachis hypogea*) or even grasses like *Cenchrus pedicellatus* which are C4 plants.

C3 photosynthesis occurs in all mesophyll cells and is a multi-step process in which the carbon from CO_2 is fixed into stable organic products. The first step involves ribulose bisphosphate (RuBP) carboxylaseoxygenase (RuBisCO) combining RuBP (5C molecule) with CO_2 to form two molecules of phosphoglycerate (3C molecule). However, C3 plants do also lose a portion of their fixed CO_2 to oxidative photorespiration under present CO_2:O_2 ratios because RuBisCO is also an oxygenase (Ehleringer and Bjorkman 1977; Ehleringer et al. 1997; Sage and Kubien 2007). Experimental evidence has strongly supported the theoretical prediction that at current CO_2 levels, C3 plants are more CO_2-limited than C4 species and thus will respond more to rising CO_2 (Ehleringer and Bjorkman 1977; Ehleringer et al. 1997; Ehleringer and Cerling 2002).

In C4 plants, the C-accumulation strategy minimizes photorespiration through anatomical and biochemical specializations that concentrate CO_2 at the active site of Rubisco (Ehleringer and Cerling 2002; Sage 2004) and are virtually CO_2 saturated already at current CO_2 (aCO_2). C4 plants, use a different enzyme (phosphoenolpyruvate carboxylase) lacking oxygenase activity and having a high affinity for CO_2 to first incorporates CO_2 into a 4-carbon intermediate (Hatch and Slack 1966), which is then transferred to specialized bundle sheath cells where CO_2 is released, resulting in locally high CO_2 concentrations. In the bundle sheath cells, RuBisCO catalyzes carboxylation, but with low rates of photorespiration because of the high CO_2:O_2 ratios and the Calvin-Benzen cycle continues as in C3 plants.

In many studies, plants mainly have two responses to elevated atmospheric carbon dioxide concentrations by (1) increased growth and biomass accumulation (Drake et al. 1997; Wand et al. 1999; Ainsworth and Long 2004) and (2) a reduction of stomatal conductance, which leads to an increased C-uptake per transpired H_2O (water use efficiency, WUE) (Leakey et al. 2012). However, C4 plants are proven to be less limited by ambient atmospheric CO_2 concentrations than C3 plants, and thus respond less to elevated CO_2 concentrations (Ehleringer et al. 1997; Wand et al. 1999; Ainsworth and Long 2004; Sage and Kubien 2007). Recent results from long time FACE experiments indicate however that biomass of C3 grasses were markedly enhanced at eCO_2 in the first 12 years, but the reverse was the case in the subsequent 8 years citing a reversal of N-mineralization (Reich et al. 2018). Kgope et al. (2009) have reported CO_2 to cause increases in tree species in savanna ecosystems and even suggested that eCO_2 could lessen the effect of fire and herbivore regimes that were effective in controlling trees in savanna ecosystems. However, Higgins and Scheiter (2012) show that eCO_2 will force transitions to vegetation states characterized by higher biomass and/or woody-plant dominance. Notwithstanding the many reports of how elevated carbon dioxide influences tropical trees and grasses, studies on effects of increased CO_2 on agroforestry parklands are scarce and the effects on shea and one of its major competitors kyasuwa (C4 grass) have not yet been tested experimentally.

1.2.2 The inter-play of grass and tree species in savanna ecosystems

A unique ecological feature of savannas is the co-existence of grasses and trees (Scholes and Archer 1997). Tree-grass competition is a fundamental driver of vegetation dynamics in savannas (Scholes and Archer 1997; Bond 2008). The tree–grass interactions in savannas have been investigated with regards to competition for water and nutrients (Scholes and Archer 1997; Jeltsch et al. 2000; House et al. 2003; Sankaran et al. 2005). Grasses are reported to intensely compete with trees at various demographic stages (Riginos 2009). However, their effects are most severe at the tree seedling stage (Cramer et al. 2009, 2010) when grasses can limit the ability of trees to recruit into saplings and more established size classes, particularly by competition for light, water and nutrients (Davis et al. 1999; Higgins et al. 2000; Midgley and Bond 2001; Vadigi and Ward 2013). Previous research on biotic interactions of shea trees with other plant species mainly focused on interactions with food crops in agroforestry systems reporting positive effects of bi-cropping on soil fertility and/or micro-climate and negative effects of shea shading on crop yield (Bayala et al. 2002, 2008b; Bazié et al. 2012; Boffa 2015; Bayala et al. 2015). However, Baziari et al. (2017) reported no direct shading effect of shea trees on crops, but higher soil moisture of the shaded area leading to higher crop yield.

Campbell and Holdo (2017) reported C4 grasses out-competing African savanna tree seedlings resulting in drastic reductions in tree carbon assimilation rates. C4 grasses are also described to suppress the growth of woody species (Cramer et al. 2010; Holdo and Brocato 2015) with Ketter and Holdo (2018) emphasizing the importance of belowground grass competition eliciting physiological responses of tree seedlings. Competition with tall grasses also has the ability to induce shade on tree seedlings which reduced the light intensity received by woody plants and thereby affecting the light acclimation of photosynthesis.

1.2.3 The role of water availability (rainfall) in savannas

Rainfall is highly variable across the continent Africa, and its amount mainly controls the location of the major biomes; tropical forest, savanna and desert and also the different types of African savannas (Walter 1971; Shorrocks 2007). Apart from the amount of rainfall, the seasonal distribution and whether there are one or two rainy seasons and also the length and severity of the dry season are all vital to determine the structure of vegetation, especially tree establishment. Savanna areas generally have a positive water regime (rainfall greater than evaporation) during the wet season and a negative balance during the dry season (Walter 1971; Shorrocks 2007). The two main life forms (grass and trees) deal with water availability through their hydraulic strategies.

Mean annual rainfall is known to limit tree cover in African savannas (Good and Caylor 2011; Greve et al. 2011). C4 grasses are still limited by water shortage despite the high carbon uptake per unit water loss because water availability is critical to C4 productivity. Grasses generally escape drought as deciduous perennials and are mostly active in the wet season while surviving the drought stress as seeds or being dormant (Ludlow 1980). A common indicator of water stress in C4 grass is leaf rolling (Chandra and Dubey 2009; Cardoso et al. 2015). However, to deal with drought stress C4 grasses generally employ deep root systems to reach lower layers of water table (Guenni et al. 2004; Zhou et al. 2013, 2014). There are also C4 grasses that engage in the development of extensive root systems to maximize water capture and also minimize leaf area to reduce leaf transpiration (Zhou et al. 2012; Cathey et al. 2013).

Woody species of the savanna have varied and complex hydraulic strategies. Some trees tend to be drought-resistant, exhibiting isohydric behavior, a conservative strategy limiting transpiration rates and stomatal conductance during periods of water stress to maintain water potential (Bucci et al. 2005), and buffering water supply through tissue water storage (Scholz et al. 2007, 2008). Other tree species are either drought-avoiders i.e. deciduous species with sophisticated root morphology to maximize resource capture during a limited growth season (Meinzer et al. 1999). There are also evergreen drought-resisters that minimize transpiration rates and cavitation risk to persist under dry conditions (Poorter and Markesteijn 2008; Markesteijn and Poorter 2009). Some species (e.g. shea) in addition to one of these strategies also exhibit hydraulic redistribution where water is moved from the relatively wetter deeper layers to the drier upper soil profile (Bayala et al. 2008a).

1.2.4 The effect of fire in savannas

Patterns of fire severity are influenced by factors like topography, weather, and fuels (Estes et al. 2017). In the savanna, the long periods of drought (4-7 months) with the predicted increases in temperature as a result of climate change causes the grasses/ herbaceous layer that typically has shallow roots to dry up producing huge amounts of combustible materials (fuel). The fires are therefore typically grass-fueled surface fires and rarely spread through the canopies of the trees. Fires are an annual recurring factor in savannas which are suggested to help maintain grassy vegetation where the climate is suitable for woodlands or forests (Bond and Midgley 2012). Mouillot and Field (2005) have reported C4 grassy biomes to support the highest fire frequencies on Earth. These fires are, apart from their effects on plant vegetation and soil, a major source of many trace gases like carbon monoxide on a regional and a global scale (Duncan 2003). Effects of fire on vegetation differ from mammalian herbivory as it unselectively defoliates vegetation irrespective of quality and any adaptations to herbivory. Fires can thus be seen as ‘general’ herbivore (Bond 2005). Human-made fires are closely related to land use and there are many reasons for setting them (Andreae 1992).

The establishment of woody plants in fire-prone tropical savannas is affected by the frequency of fires and the growth rates of seedlings of the occurring trees. Seedlings can only establish if they achieve sufficient stem diameter/height to survive the next fire (Higgins et al. 2000; Bond 2008). In ecosystems with frequent fires or slow growth rates, woody plants may not be able to escape this “fire trap” despite increases in moisture availability (Shanahan et al. 2016). Savanna fires typically burn the herbaceous layer, with tree seedlings and saplings not tall enough to escape the flames experiencing top kill (partially or wholly destruction of aboveground biomass) (Williams et al. 1999; Higgins et al. 2012). Although top kill in savannas fires scarcely leads to plant death (Bond and van Wilgen 1996; Hoffmann et al. 2009), repeated top kill either leads to death or demographic bottleneck with a large number of trees and saplings unable to reach canopy height (Bond and van Wilgen 1996; Higgins et al. 2000, 2012; Bond and Keeley 2005). In fire-prone regions like the savanna, woody plants recover after fire by resprouting from insulated aerial or subterranean buds (Lamont et al. 2011). Depending on the severity of the fire, plants may resprout from sunken accessory buds on main/swollen stems (Burrows 2002; Klimesˇová and Klimeš 2007) or rootstocks/lateral roots (Chattaway 1958; Lamont and Barrett 1988) or buds located in the leaf axils of twigs (Cremer 1972) or even from primary axillary buds on rhizomes (Witkowski and Lamont 1997).

1.3 Objectives and chapter outline

The main research question addressed in this thesis is; how global change factors (atmospheric carbon dioxide concentration, grass competition, water availability and fire) affect shea and kyasuwa growth, biomass allocation and nutritive value. The specific objectives were (1) to review literature of current knowledge on shea and research gaps of this important tree species, (2) to quantify the effects of elevated CO_2 and water availability together with fertilization regimes on kyasuwa biomass allocation and nutrients content, (3) to investigate the effect of elevated $CO_{2,}$ water availability and grass competition on shea seedling growth and (4) to evaluate the effect of fire on initial growth, biomass allocation and the partitioning of carbon and nitrogen in shea organs. The central hypothesis of my thesis is that global change drivers interact to elicit plant-trait responses in shea and kyasuwa and don't act in isolation.

Chapter 2: Shea (*Vitellaria paradoxa* C. F. Gaertn.) at the crossroads: Current knowledge and research gaps

Shea (*Vitellaria paradoxa* C. F. Gaertn.) is arguably socio-economically and environmentally the most important plant species in the semi-arid and arid zones of Africa where it is widely distributed. The review in chapter 2 of this thesis summarizes the current knowledge of the morphological and genetic diversity; propagation, initial growth, and management; ecology and population structure; chemical and nutritional composition and the socioeconomic and livelihood empowerment potential of shea. The review also reveals that little is known about the fruiting behaviour and the responses of shea to the inevitable changes in climate and therefore suggests eco-physiological and dendrochronological studies as an option to predict how the domestication of this multipurpose tree species can be sustained even under the prospects of global change.

Chapter 3: Effects of elevated carbon dioxide and climate change on biomass and nutritive value of kyasuwa (*Cenchrus pedicellatus* Trin.)

Kyasuwa grass is an important grass component of many savannas. Atmospheric carbon dioxide enrichment may enhance plant growth and development and may alter the nutritive value of grasses. *Cenchrus pedicellatus* (Trin.) belongs to the Poaceae family and is native to West Africa where it grows along shea in parklands. The purpose of this work was to determine the effects of future elevated atmospheric CO_2 concentration on biomass partitioning and nutritive value of kyasuwa grass. The objectives of the study were (1) to assess the effects of eCO_2 on kyasuwa growth, biomass allocation and nutritive value, (2) to evaluate how different water and fertilization regimes affect kyasuwa growth, biomass allocation and nutritive value and (3) to estimate interactive effects of the three resource factors on these traits of kyasuwa.

Chapter 4: Elevated CO_2 does not offset effects of competition and drought on growth of shea (*Vitellaria paradoxa* C.F. Gaertn.) seedlings

The inter-play of abiotic conditions (e.g. rainfall patterns, drought periods) and biotic interactions (grazing by large herbivores) shape parklands because they influence vital processes like photosynthesis, transpiration and biomass production of common plant species including shea. The main objective of this experiment was to assess the extent to which performance of shea seedlings (in terms of growth and biomass production) are affected by increases in atmospheric concentrations of CO_2, and how the effects of eCO_2 on shea would be modulated by competition with the C4 grass *Cenchrus pedicellatus* and by water availability.

Chapter 5: Excellent shea (*Vittelaria paradoxa* C.F.Gaertn.) seedlings recovery after fire: gas-exchange, growth and biomass partitioning

Fire can be seen as a generalist herbivore of vegetation and is presumed to be intensified by climate change. Shea (*Vitellaria paradoxa* C.F. Gaertn) is native to the savanna ecosystem which is prone to periodic bushfires because of the long dry season and accumulated combustible biomass mostly grass. The main objective of this study was to assess the processes that are crucial to understanding the mechanisms that facilitate shea productivity and adaptation to the savanna environment. The specific objectives of the study were (1) to assess shea seedlings gas exchange after simulated fire and (2) to evaluate the effect of simulated fire on shea seedlings growth and biomass allocation.

Box 1: Allocation patterns of carbon and nitrogen in shea (*Vitellaria paradoxa* C.F.Gaertn.) after simulated late burning

Fire is a global biogeochemical agent, influencing vegetation structure (Bond & Keeley, 2005) and carbon cycling in parklands. Savanna ecosystems are prone to annual wildfires because of the long periods of drought and high combustible material in the form of grass, shrubs and fallen tree parts. We studied the effects of simulated late burning on the shea's vigor by investigating the allocation patterns of carbon and nitrogen in seedlings measuring leaf pigments, carbon and nitrogen content of organs and C stable isotope ratios in unburnt (control) and regrowths after burning.

CHAPTER TWO


Shea fruits
Shea butter & products
cantu
shea butter
NEW!
NATURAL HAIR
curling cream

2 SHEA (*VITELLARIA PARADOXA* C. F. GAERTN.) AT THE CROSSROADS: CURRENT KNOWLEDGE AND RESEARCH GAPS

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2.1 Abstract

Shea (*Vitellaria paradoxa* C. F. Gaertn.) is arguably socio-economically and environmentally the most important plant species in the semi-arid and arid zones of Africa where it is widely distributed. Apart from the economic gains in international export markets where shea butter is valued for use in luxury cosmetic, pharmaceutical and confectionary industries, locally the fat (butter) is the main cooking oil for over 86 million inhabitants. Research during the past decades has acknowledged the chemical and nutritional composition as well as the ethnobotanical uses of shea which has resulted in its butter being used in a wide array of products. This review summarizes the current knowledge of the morphological and genetic diversity; propagation, initial growth, and management; ecology and population structure; chemical and nutritional composition as well as the socioeconomic and livelihood empowerment potential of shea. Little is known about the fruiting behaviour and the responses of shea to the inevitable changes in climate. We suggest ecophysiological and dendrochronological studies as an option to predict how the domestication of this multipurpose tree species can be sustained even under the prospects of global climate change.

Keywords: Shea, climate change, parkland, savanna and ecophysiology

2.2 Introduction

The shea tree (*Vitellaria paradoxa* C. F. Gaertn., synonyms: *Butyrospermum paradoxa* (C. F. Gaertn.) Hepper. or *Butyrospermum parkii* (G. Don.) Kotschy.), is native to the savanna belt of the Sudanian region centre of endemism from Senegal to the foothills of the Ethiopian highlands (White 1983) covering a 6,000 km belt (Okullo et al. 2004; Sanou et al. 2006) across 21 countries (Boffa 2015; Naughton et al. 2015) as shown in Fig. 2.1. Except in Ghana and Nigeria, where it occurs within 50 km off the coast, shea is generally an inland tree (Hall et al. 1996). It belongs to the plant family Sapotaceae and is the only species of the genus *Vitellaria*. Two sub-species are recognised: *V. paradoxa* subsp. *paradoxa* found in West and Central Africa (from Senegal to the Central African Republic) occurring at elevations of 100-600 m above sea level (Hall 1996; Boffa 1999) and *V. paradoxa* subsp. *nilotica* in Eastern Africa (Ethiopia, Sudan, Democratic Republic of Congo and Uganda) which occurs at higher altitudes between 1200-1600 m above sea level, except for a few populations in Sudan at 500 m (Vermilye 2004; Okullo et al. 2004; Byakagaba et al. 2011). A geographical distance of 175 km separates the two sub-species along the different watersheds in the area: the Lake Chad basin is home to subsp. *paradoxa* and the Nile drainage basin is home to subsp. *nilotica* (Hall et al. 1996). Analyses of genetic diversity of shea trees across Sub-Saharan Africa have indicated the Adamawa Highlands along the border of Cameroon and Nigeria as the geographical divider of the two sub-species rather than the watersheds (Allal et al. 2011).

The deciduous, medium size tree attains a height of 10-20 m, occasionally reaching 25 m (Maydell 1990; Yidana 2004) and stem diameters between 0.3-1.0 m (Chevalier 1946). It is a slow-growing tree and generally produces smaller and fewer fruits from 15 to 20 years of age, with maximum fruit production after 25-40 years of growth (Sanou et al. 2004). Shea tree can reach an age of up to 300 years (Delolme 1947; Ruyssen 1957; Jøker 2000). The elliptically shaped fruit is 4-8 cm long and 2.5-5 cm wide (Hall et al. 1996; Moore 2008) and weighs 10–57 g with an annual production of 15-30 kg per tree (Greenwood 1929; Ruyssen 1957; Agbahungba and Depommier 1989). The fruit is highly nutritious with a thin fleshy pericarp which has a sweet pear-like taste enclosing the oval, reddish-brown seed, the so-called ‘shea nut’. The seed has a shiny, smooth surface and constitutes about 50 % of the weight of the fresh fruit (Maranz and Wiseman 2003). The pericarp of the ripe fruit is eaten by both humans and livestock. Parts (bark, roots, wood) of the tree are used for medicine, construction materials, fuel wood and carving wood (Hall et al. 1996; Boffa 1999). The shea tree is highly valued by farmers, mostly because of its fatty acids rich seeds which are sold both locally and internationally. The commercialization of shea products represents an important source of income for the local community and even entire countries such as Burkina Faso and Ghana (Bonkoungou 1992; Elias and Carney 2007; Moore 2008).

Internationally in the export market, shea butter is valued for use in luxury cosmetics or pharmaceutical goods. Roughly 90 % of export volume goes for confectionary applications and 10 % for cosmetic uses (Rousseau et al. 2015). Between August 2014 and September 2016, the Global Shea Alliance facilitated the export of 121,000 MT dry shea kernels with a market value of US $43 million from Africa (GSA 2016). Due to the economic importance of the species, an up-to-date summary of the knowledge and research carried out on shea is needed.

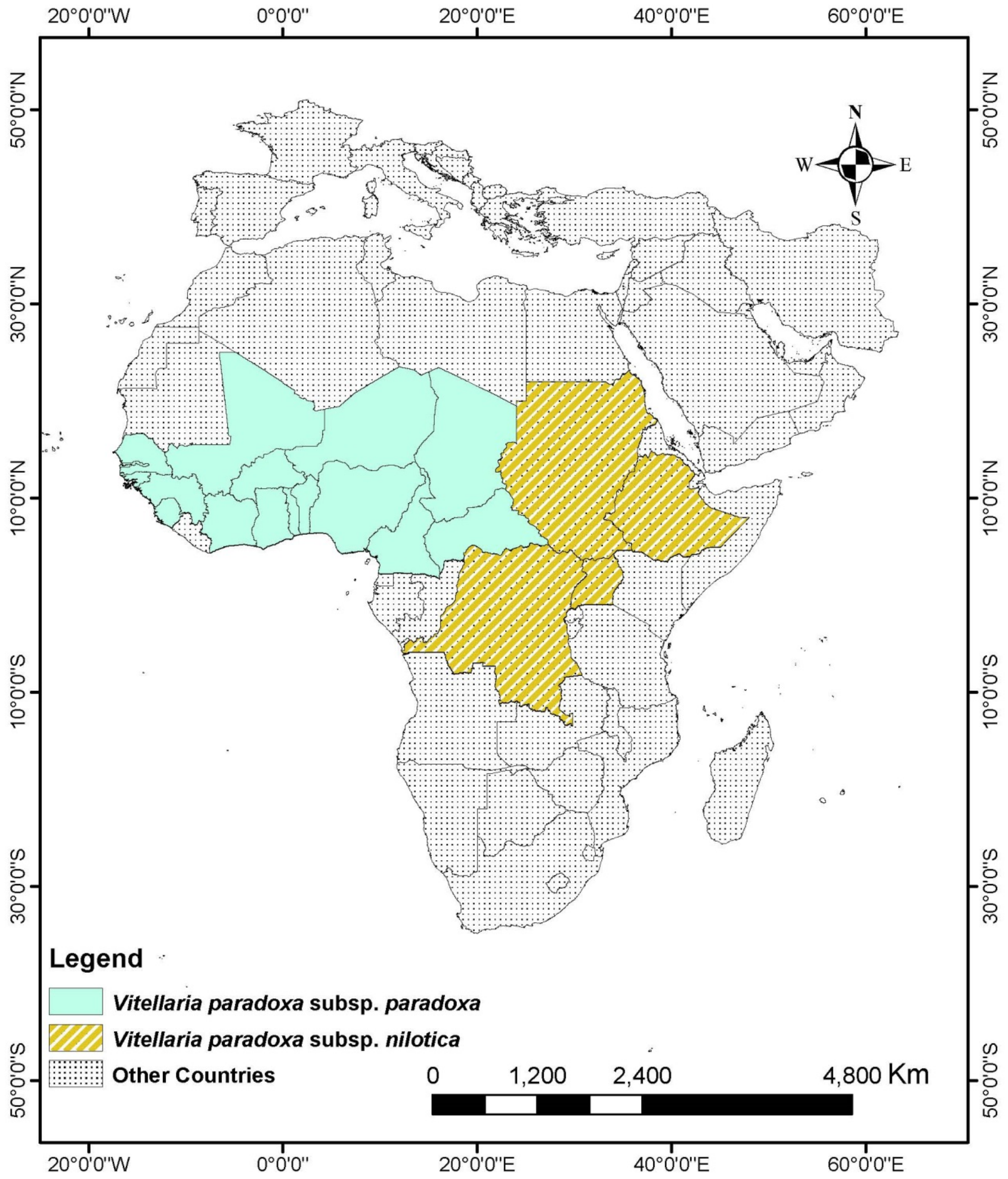

Fig.2.1 Distribution map of shea showing the occurrence of the two sub-species (Source: Damian Tom-Dery)

Research so far covers predominantly ethnobotanic utilization as well as the chemical and nutritional quality (Chavalier 1946; Ruyssen 1957; Bonkoungou 1987; Abbiw 1990; Hall et al. 1996; Maranz et al. 2004a; Maranz and Wiesman 2004; Honfo et al. 2014). We review state-of-the-art knowledge of the morphology and genetic diversity; germination and initial growth; ecology and population structure; chemical composition and nutritional values; and socio-economic and poverty alleviation potential of shea. We also seek to identify knowledge gaps and explore future research possibilities into the adaptation of shea to climate variables in this era of global climate change.

2.3 Morphological characteristics, Genetic diversity and domestication

The unique socio-economic and ecosystem services provided by shea have elevated it into the priority list of African genetic resources (FAO 1988). Though the species is wild, it can conveniently be termed a semi-domesticated species because of centuries of association with humans and the resultant anthropic selection the species has undergone (Pullan 1974; Lovett and Hag 2000a). The leaves and flower parts (sepals, filaments and styles) of subsp. *nilotica* are larger compared to subsp. *paradoxa* (Osei-Amaning 1996). The shape of nuts of subsp. *nilotica* are described as oval (Eggeling and Dale 1951) while that of subsp. *paradoxa* are described variously as spherical, ovoid and fusiform (Ruyssen 1957). High intra-specific variation exists among shea trees from different African regions (Chevalier 1948; Ruyssen 1957; Lovett and Haq 2000b; Sanou et al. 2006; Diarrassouba et al. 2006; Ugese et al. 2010b; Okullo 2011; Gwali et al. 2011; Gwali et al. 2012a; Enaberuel et al. 2014; Djekota et al. 2014; Souberou et al. 2015). The leave and fruit characteristics of shea across its geographical range are illustrated in Table 2.1.

Understanding the variability within the gene pool of shea is crucial to facilitate its domestication, conservation and future improvements. Lovett and Hag (2000b) suggested with isoenzyme analysis of shea from Ghana, the existence of moderate to high heterozygosity and high gene flow. They inferred that past climatic changes and nonexistent methods of seed selection were the causes. They also proposed seed and leaf lamina shape as possible indicators of genetic diversity. There have also been studies of shea genetic variability using biochemical composition by analysing for fatty acids (Maranz and Wiesman 2003; Maranz et al. 2004b; Di Vincenzo et al. 2005; Allal et al. 2013), phenolic compounds (Maranz et al. 2003) and tocopherols (Maranz and Wiesman 2004; Allal et al. 2013).

Table 2.1 Morphological characteristics of shea leaves and fruits in various countries

Country	**Leaves (cm)**		**Fruits (cm)**		**References**
	Length	Width	Length	Diameter	
Ghana	9.2-22.5	3.7-5.2	1.7-3.7s	1.7-2.7 ws	Lovett & Hag 2000b; Moore 2008; Nyarko et al. 2012; Issaka 2013
Benin	17.3-19.4	7.0-7.2	4.3-4.7	3.4-3.7	Souberou et al. 2015
Nigeria	12.8-17.3	5.3-7.7	3.9-5.2	3.2-3.7	Ugese et al. 2010c; Okullo et al. 2011; Enaberuel et al. 2014
Mali	13.7-14.9	3.9-4.9	3.6	3.1	Sanou et al. 2006
Chad	15.5-26.3	3.0-5.4	1.0-3.3	2.3-4.4 w	Djekota et al. 2014
Cameroon	10.0-25.0	4.0-12	3.7-8.2	2.9-5.3	Vivien 1990; Diarrassouba et al. 2006
Uganda (sspn)	28.69	8.6-9.2	2.95s	2.06 s	Gwali et al. 2011

w (width), s (seed), sspn (sub-species *nilotica*)

Microsatellite DNA has widely been utilized in population genetics because of its ability to detect differences among closely related species. Kelly et al. (2004) used ten microsatellite loci to examine the effect of anthropogenic activity on the spatial and temporal genetic structure of shea population, concluding that differentiation was very limited at the microsatellite loci, perhaps because of the buffering effect of extensive gene flow between unmanaged and managed populations. Microsatellites have been used to illustrate within population diversity (Sanou et al. 2005) and to differentiate between ethno-varieties (Gwali et al. 2015). Past climatic conditions and anthopogenic activities have been cited as the causes of these variations. Random amplified polymorphic DNA (RAPD) and chloroplast markers analysis from several populations distributed across West and Central/Eastern Africa suggested genetic distinction between West and Central/Eastern African populations (Fontaine et al. 2004; Bouvet et al. 2004; Allal et al. 2011). Recognising there are distinctive gene pools between the two sub-species occurring in different regions implies they might differently adapt to future climate changes. The diversity of the shea gene pool within and between countries and even regional populations calls for a concerted organized collection and assessment of superior germplasm, building on previously separated stand-alone research across the region (Boffa 2015).

2.4 Shea propagation, initial growth and management

Typical for shea as an indigenous savanna species is its demand for light, especially in the early years of growth. Seed dispersal is mainly by birds, ungulates and primates, including humans that eat the fruits. Long distant seed dispersal is mostly by fruit bats (Fujita 1991; Djossa et al. 2008a). The phenological events of shea are timed with regards to seasons; leaf fall, leaf flushing and flowering (December-March) are notably dry season events while fruiting (April-September) coincides with the raining season (Jøker 2000; Okullo et al. 2004). The maturing of fruits and ripening during the rainy season possibly is an adaptation for maintenance of the species (Okullo et al. 2004) because the seeds are recalcitrant (Hall et al. 1996; Jøker 2000) with seed viability generally limited to a week and at most a month (Ruyssen 1957) depending on storage conditions (Jøker 2000). Fallow periods offer shea opportunities for regeneration, but these are continuously being shortened because of pressure for land (Boffa 1999; Lovett & Haq 2000a) and land hunger. The wild species traits that impede shea cultivation include problems with germination (Jøker 2000; Ugese et al. 2005), the extended gestation period (Awoleye 1995) and slow growth rate (Jackson 1968) which makes its cultivation less attractive to farmers (Yidana 2004).

Although in savanna ecoregions shea regenerates unaided, the complete process of germination is cumbersome because the seed looses its viability quickly and it takes a long period for the shoot to emerge which is a major challenge for shea to be planted by farmers. The peculiar germination and seedling morphology of shea is described as cryptogeal (Fig.2.2) and involves the burying of the plumule (Jackson 1968). The fallen seeds as a result of its shape turn to have the scar area facing downwards to enable water uptake. This causes the testa to crack towards the micropyl and the pseudo-radicle which is positively geotropic emerges and grows into the soil. This grows to a depth of 7-8 cm before a swelling arises at 5-7 cm away from the testa, which splits for the shoot to emerge and push upwards. The pseudo-radicle continues to grow and develop into the tap root (Osei-Amaning 1996). After germination the shea seedling first produce a long tap root before growing any leaves (Yayock et al. 1988) which can be considered as an adaptive mechanism against drought. Frimpong and Adomako (1987) established that about 74 % of the dry matter of seedlings is found in their roots, indicating that shoot development is suppressed in the early stages of shea seedling growth. The time it takes for the appearance of the shoot above ground when seeds are planted takes between one to more than two months under favorable conditions (Delome 1947; Ruyssen 1957; Awoleye 1995; Jøker 2000; Yidana 2004; Ugese et al. 2005; Ugese 2010). Depulping is known to facilitate seed germination (Ruyssen 1957; Osei-Amaning 1996), while optimal and uniform germination as well as seedling production is enhanced by soaking of seeds in concentrated H_2SO_4 for 10 min or Stenberg solution and removing the seedcoat (Jatto et al. 2012; Iroko et al. 2013; Iddrisu 2013). Early seedling emergence correlates with faster growth rates (Ugese 2005) and seed size is positively correlated to emergence, growth and seedling development (Kolawole et al. 2011).

Fig. 2.2 Cryptogeal germination of shea showing the burying of the plumule (Source: Damian Tom-Dery)

Grafting as a vegetative means of propagation is defined by Sanou et al. (2004) as ‘a method of vegetative propagation that allows the production of individuals of the same genetic constitution as the original plant, and hence facilitates the multiplication of desirable genotypes’. This can be employed to improve the development of trees in the reproductive stage (Grolleau 1989; Hartmann et al. 1997), by taking scions from the ontogenetically mature crowns of older trees and thereby avoiding the extended juvenile phase (Hackett 1985; Hartmann et al. 1997). Grafting as a method of achieving early maturity on four year old shea seedlings was reported to have a success rate of only 25 % due to the wilting of the scions in dry and hot conditions of the Sahel (Groulleau 1989). Even with successful grafts, fruit production has been shown to be restricted (Kambou 2001; Sanou et al. 2004).

Experiments with stem cutting propagation of shea have reported that root formation depends on the concentrations of applied phytohormones (Zerbo 1987; Bonkoungou et al. 1988; Frimpong et al. 1993; Yidana 2004; Yeboah et al. 2009; Yeboah et al. 2011). Up to a 100 % survival after planting of cuttings was reported depending on the time of the year and the environmental conditions (Opoku-Ameyaw et al. 1997). Developing in vitro systems for shea shoot and root regeneration of explants taken from mature materials might aid in shortening the long juvenile phase. However, rather few efforts in the somatic embryogenesis of shea calli have been made, and shoot or root production has been successful in some cases (Fotso et al. 2008; Adu-Gyamfi et al. 2012; Lovett and Hag 2013). Yeboah et al. (2014) found in survival trials that, the mist propagator was the most appropriate propagating structure for weaning rooted cuttings with planting depth of 52 cm producing higher survival rates and better growth. They also suggested the beginning of the rainy season for establishment, as this is vital for the survival of transplanted propagules.

Layering, which is generally the growth of roots on a stem while the stem is still attached to the mother plant, has achieved minimal but nevertheless encouraging results. Zerbo (1987) and Bonkougou et al. (1988) reported 2 % survival for air layering and 15 % for ground layering during the raining season using substantial amounts of hormones. This technique has the advantage that the resulting plants grow better than those directly from seed, thus air layering with epicormic shoots produced roots within 51 days (Yidana 2004). Also a container layering technique holds promise for the rooting of shea trees with rooting performance of 40.9 % for four year-old seedlings and 27.9 % for mature shea trees (Amissah et al. 2013). Pruning has no effect on shea growth (Kessler 1992), nevertheless in agroforestry systems it increases yield of inter crops like millet (Bayala et al. 2002) and is recommended to farmers as a way to rejuvenate aging trees (Bayala et al. 2008a). Girdling as a method to regulate fruiting irregularity is reported to increase fruit yield by 100 % (Lamien et al. 2006).

Water logging has detrimental effects on seedling growth (ICRAF 2000) but wide spacing, good site preparation and weeding are vital for plant survival (Jøker 2000). There are conflicting reports of the response of shea growth to NPK fertilization. Shea growth has been shown to benefit from residue effects of NPK fertilizers applied to the intercropped foods in rotations of maize, cowpea and yam (Osei-Bonsu et al. 1995). Seedlings grown in N and P deficient sand cultures recorded stunted growth (Dianda et al. 2009; Ugese et al. 2012). In contrast, Yakubu et al. (2015) reported no significant effect of NPK fertilization on seedling growth. Shea propagation needs protection from herbivore grazing (Chevalier 1946) and competing vegetation (Delome 1947). Neighbouring grasses are not only competitors for space, light and nutrients but also a source of combustible matter which intensifies the periodic bush fires (Osei-Amaning 1996). Phytosanitary problems associated with shea include the larvae of *Mussidia nigriolla* and *Ceratitis silvestrii* feeding on the pulp of fruits (Jøker 2000). A plant hemiparasite of the genus *Tapinanthus* (African mistletoe) is a major cause of tree mortality by reducing the growth of the distal ends of the branches, thereby affecting wood quality and increasing susceptibility to attack by pathogens (Hall et al. 1996). The shoot and fruit borer *Salebria* sp. infests mostly the reproductive phenophases of flowering and fruit production (Lamien et al. 2008).

2.5 Tree ecology, distribution and population structure

Shea preferably grows in loamy and sandy soils but not clayey, anaerobic, volcanic soils; however the soils should be well drained with a good water-holding capacity (Hall et al. 1996; Moore 2008; Naughton et al. 2015). There are reports of a significant correlation of sand content and phosphorus levels to tree density (Moore 2008). Annual leaf abscission probably plays a major role in nutrient recycling through the decay of leaves and fine roots at the soil surface (Bayala et al. 2006). The species generally thrives in the arid and semi-arid areas where annual rainfall amounts range between 400-1500 mm (Maydell 1990; Hall 1996) and it tolerates an extended drought of up to eight months (Vermilye 2004). Agroforestry parklands (Fig. 2.3) defined as a dispersed arrangement of scattered trees within which annual crops are cultivated (Pullan 1974; Boffa 1999) are considered the most widespread farming system in the Sahelian zone (Bayala et al. 2015). In these parklands, shea trees constitute a high-percentage of standing biomass thereby protecting the environment against soil degradation and possessing significant carbon stores with high potential for future C-sequestration for climate change mitigation (Luedeling & Neufeldt 2012). Shea also has the ability to clean-up atmospheric pollutants and is thus recommended for use in green belt development (Ogunkunle et al. 2015).

Few studies have investigated shea phenology, with Okullo et al. (2004) reporting that, for sub-species *nilotica*, the pattern of leafing and leaf loss, flowering and fruiting are unimodal although rainfall is bimodal in the studied area. However, Kelly et al. (2007) investigated the effect of human practices on the flowering of sub-sp. *paradoxa*, concluding that cultivated fields provided better conditions for flowering than fallow lands and there was a positive correlation of flowering and fruiting with higher rainfall. Lamien et al. (2007) reported higher fruit yields in highland than lowland shea populations and were able to simultaneously predict number of fruits, fruits fresh and dry weights with selected dendrometric and fruiting variables. Bushfire during flowering has a negative effect on fruiting (Chevalier 1948; Ruyssen 1957; Abbiw 1990) while harmattan winds cause flower abscission (Ruyssen 1957). Delolme (1947) reported the amount and timing of rainfall to slightly impact fruit maturation, but Ruyssen (1957) found no correlation between rainfall and fruit yield. On the contrary, Glèlè Kakaï et al. (2011) reported that high rainfall and relative humidity reduced fruit production. There are also suggestions that fruit set formation is limited by pollination (Osei-Amaning 1996). It is, however, generally accepted that fruit production is cyclical with 2-3 year cycles (Delolme 1947; Agbahungba and Depommier 1989; Masters 2002; Yidana 2004).

Research is, required on the effects of annual climatic conditions, future projected climate variations (increased atmospheric CO_2 concentration and increased global average temperatures), the effects of different soil constituents and drought stress on flowering and fruit production, and the interaction of these abiotic factors with the age of shea trees.

Fig. 2.3 Shea parkland in Northern Ghana with maize grown under scattered shea trees (Source: Damian Tom-Dery)

Shea represent up to 70 % of the woody vegetation in areas of Benin (Agbahungba and Depommier 1989; Djossa et al. 2008b) and may constitute about 80 % in parts of northern Ghana (Lovett and Haq 2000a) and Burkina Faso (Boffa 1999). Shea is often the dominant species in parklands and mostly associated with tree species such as *Parkia biglobosa*, *Terminalia avicennioides*, *Acacia senegal* and *Annona senegalensis* (Boffa 1999). There is evidence of hydraulic redistribution in shea which may suggest facilitation for associated plants in parklands (Bayala et al. 2008b) and might even explain the co-existence of tree and grass in savanna ecosystems. The Sudanian savanna zone which recorded the highest population of shea trees in the 1940s with estimates of 230 trees ha^{-1} (Chevalier 1946) has decreased densities since then to only 11 trees ha^{-1}

(Nikiema et al. 2001), while West Africa has numbers dwindling to 5 tree ha^{-1} (Djossa et al. 2008b). The decline in shea populations may be due to a number of factors which include short fallow periods, inappropriate agricultural methods, annual bushfires, overgrazing and the cutting of trees for firewood and charcoal production (Lovett and Hag 2000; Djossa et al. 2008b; Byakagaba et al. 2011; Aleza et al. 2015). Population studies on shea compared populations on cultivated lands to those on fallow land, as opposed to wild populations on unmanaged spots, reporting larger trees on cultivated fields (Boffa 1995). Importantly, in these studies trees with small diameter indicating regeneration were not found, a lack of which has been used as evidence for the degradation of West African parklands (Gijsbers et al. 1994). Lovett and Hag (2000a) compared shea populations on sites with different intensities of landuse and concluded that populations in farmed parklands are a direct result of anthropic selection resulting from many centuries of traditional cultivation and fallow. Odebeyi et al. (2004) reported shea and *Parkia biglobosa* as being co-dominant with the occurrence of only big trees and regeneration, recording no saplings. Djossa et al. (2008b) reported shea trees being well preserved in parklands under traditional farming that advances the growth of young shea trees resulting in a random age distribution. The population structure as documented in the distribution pattern of trunk diameter and regeneration status of both sub-species *niloticus* and *paradoxa* are affected by land management regimes in East and West Africa, respectively (Osei-Amaning 1996; Okullo 2004; Byakagaba et al. 2011; Aleza et al. 2015). The population structure (Fig. 2.4) of shea on parklands is composed of a good adult and regeneration population with very few number of or even no saplings (Osei-Amaning 1996; Okullo 2004; Aleza et al. 2015).

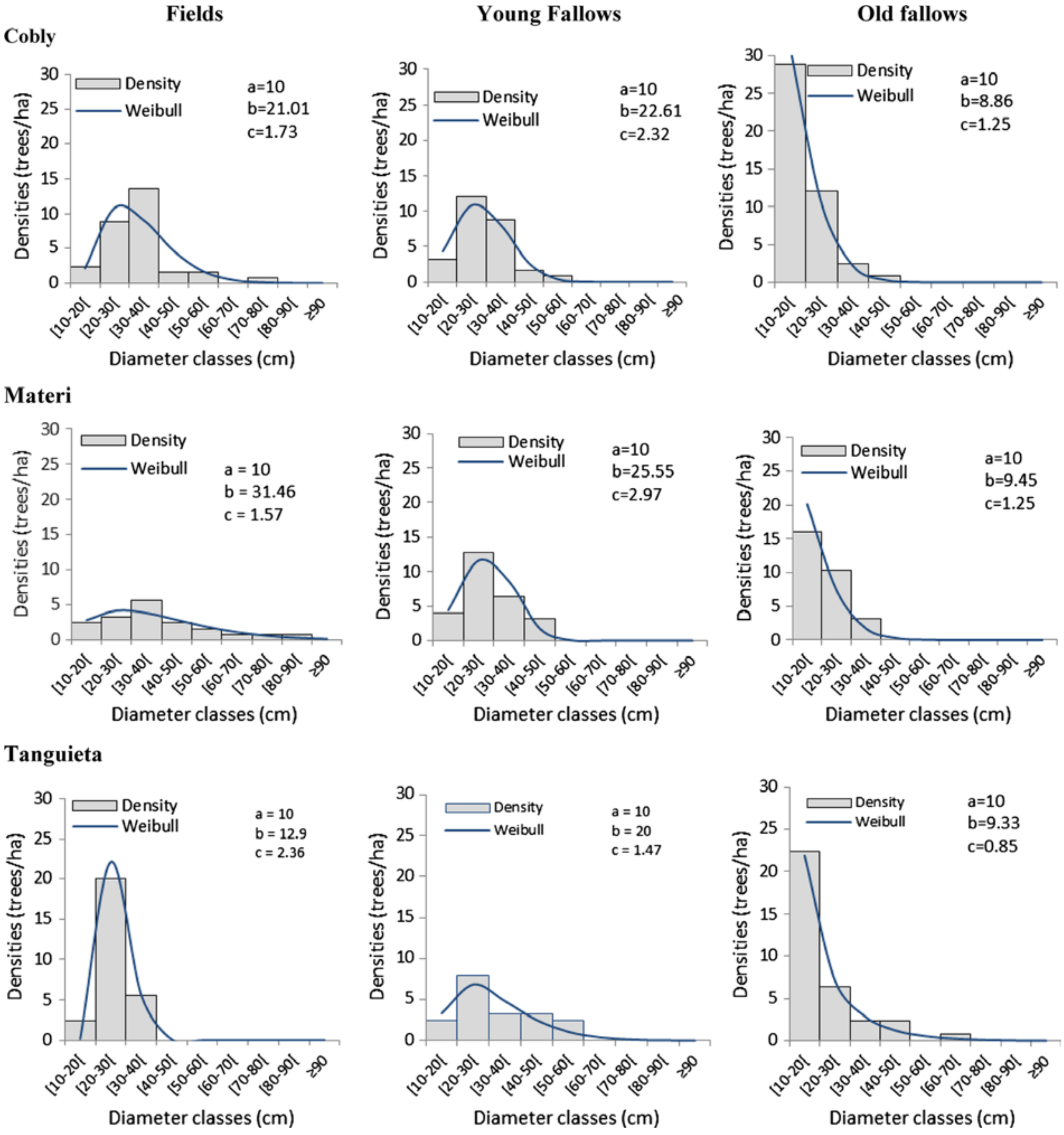

Fig. 2.4 Diameter class distribution of shea according to land use types in three localities of Benin. Source: Aleza et al. (2015)

Platts et al. (2010) used climate, topography, agro-ecological data, fire radiative power and IPCC scenarios to predict an increase in areas climatically suitable for shea in the 21st century, indicating the moisture index as the best environmental predictor of shea distribution. Therefore, shea will most likely grow in reasonably dry climates, but not too dry as in deserts. Allal et al. (2011) employed DIVA-GIS ecological niche modeling to predict the shea distribution focusing on genetic diversity and comparisons of the present distribution through the Last Glacial Maximum and last interglacial periods. The authors concluded that there was a strong geographical separation of the western and eastern populations indicating climatic variations as the major factor for the genetic patterns. Naughton et al. (2015) predicted the possible shea distribution and production using Geographic Information Systems via merging binary and suitability layers developed from eight factors (Land-use, temperature, precipitation, elevation, fire, normalized difference vegetation index, soil-type and soil drainage) concluding that the potential shea distribution area will increase in the future. Models of shea in general lack the imput of ecophysiological parameters such as properties of leaves and photosynthetic rates.

2.6 Chemical and nutritional composition

The monumental ascend in the trade of shea has led to state-of-the-art research on the chemical and nutritional properties of shea. The sweet pulp is four times richer in ascorbic acid than ripe orange (Eromosele and Kuzhhuzha 1991) and a rich source of sugars, proteins, calcium, and iron (Maranz et al. 2004a). The composition of macronutrients and minerals in the kernel and pulp of shea are illustrated in Table 2.2. Different methodology used for the analysis of the various nutrients, minerals and vitamins is a possible cause of the high variation of information about the nutritional values (Honfo et al. 2014). Shea kernels are particularly loaded with crude lipids with amounts ranging between 17.4 and 59.1 g/100 g dw (Tano-Debrah and Ohta 1994) and also contain a considerable amount of carbohydrate in the range 25 g/100 g dw (Busson 1965) to 34.8 g/100 g dw (Tano-Debrah and Ohta 1994). The pulp is rich in potassium (K) that varied between 21.7 mg/100 g dw (Mbaiguinam et al. 2007) and 1686 mg/100 g dw (Maranz et al. 2004a) while calcium (Ca) ranged between 2.5 mg/100 g dw (Ugese et al. 2008b) and 426 mg/100 g dw (Maranz et al. 2004a), representing the two most abundant nutrients found in the pulp.

The most treasured product of the shea tree is its butter extracted from the kernels which is not only highly valued by the confectionary and pharmaceutical industries but also used locally for culinary purposes. The solidified shea oil is referred to as 'butter' which consists basically of tryglycerides (stearic acid, oleic acid).

Table 2.2 Chemical and nutritional composition of the kernels and pulp of shea (Extracted from: Honfo et al. 2014)

Micronutrient	Kernels	References	Pulp	References
Crude lipids (g/100g dw)	17.4-59.1	Greenwood 1929; Busson 1965; Tallantire & Goode 1975; Duke & Atchley 1986; Tano-Debrah & Ohta 1994; Maranz & Wiesman 2003; Di Vincenzo et al. 2005; Mbaiguinam et al. 2007; Nkouam et al. 2007; Akihisa et al. 2010a	1.3	Ugese et al. 2008a
Carbohydrate (g/100g dw)	25.0-34.8	Greenwood 1929; Busson 1965; Tallantire & Goode 1975; Duke & Atchley 1986; Tano-Debrah & Ohta 1994; GRET 2007	8.1-37.2	Mbaiguinam et al. 2007; Ugese et al. 2008a
Crude fibre (g/100g dw)	3.2-20.4	Greenwood 1929; Ruyssen 1957; Duke & Atchley 1986; Tano-Debrah & Ohta 1994	42.2	Ugese et al. 2008a
Crude protein (g/100g dw)	6.8-9.0	Greenwood 1929; Busson 1965; Tallantire & Goode 1975; Duke & Atchley 1986; Tano-Debrah & Ohta 1994; GRET 2007	4.2-5.6	Maranz et al. 2004a
Moisture (%)	5.0-8.1	Busson 1965; Tallantire & Goode 1975; GRET 2007; Mbaiguinam et al. 2007	67.0-80.3	Maranz et al. 2004a; Mbaiguinam et al. 2007
Ash (g/100g dw)	1.8-3.0	Greenwood 1929; Ruyssen 1957; Duke & Atchley 1986; Tano-Debrah & Ohta 1994; GRET 2007	4.7-5.4	Mbaiguinam et al. 2007; Ugese et al. 2008a
Energy (Kcal /100g dw)	-	-	179.5	Ugese et al. 2008a
Vitamins (mg/100g)				
C	-	-	196.1	Eromosele et al. 1991
B	-	-	7.0	Maranz et al. 2004a
Minerals (mg/100g dw)				
Mg	142.6	Megnanou et al. 2007	11.1-129.0	Eromosele et al. 1991; Maranz et al. 2004a; Mbaiguinam et al. 2007; Ugese et al. 2008b
Ca	0.1-215.2	Tallantire & Goode 1975; Duke & Atchley 1986; Megnanou et al. 2007; Alhassan et al. 2011	2.5-426.0	Eromosele et al. 1991; Maranz et al. 2004a; Mbaiguinam et al. 2007; Ugese et al. 2008b
Na	0.9-73.9	Megnanou et al. 2007; Alhassan et al. 2011	19.3	Ugese et al. 2008b
Fe	0.01-3.1	Duke & Atchley 1986; Megnanou et al. 2007	0.4-16.0	Eromosele et al. 1991; Maranz et al. 2004a; Megnanou et al. 2007
Zn	0.9	Magnanou et al. 2007	0.5-4.0	Eromosele et al. 1991; Maranz et al. 2004a; Ugese et al. 2008b
Mn	0.1-0.7	Alhassan et al. 2011	0.5-4.0	Eromosele et al. 1991; Maranz et al. 2004a
Cu	0.3	Megnanou et al. 2007	0.0-1.1	Eromosele et al. 1991; Maranz et al. 2004a
K	0.1-0.2	Alhassan et al. 2011	21.7-1686.0	Maranz et al. 2004a; Megnanou et al. 2007; Ugese et al. 2008b
P	0.04	Tallantire & Goode 1975; Duke & Atchley 1986	1.0-71.4	Eromosele et al. 1991; Maranz et al. 2004a; Mbaiguinam et al. 2007; Ugese et al. 2008b

Table 2.3 Chemical and nutritional composition of shea butter (Extracted from: Honfo et al. 2014)

Nutrients	Butter	References
Crude lipids (g/100g dw)	75.0	Chukwu & Adgidzi 2008
Carbohydrate (g/100g dw)	22.3	Chukwu & Adgidzi 2008
Moisture (%)	0.1-8.4	Greenwood 1929; Magnanou et al. 2007; Olaniyan & Oje 2007; Chukwu & Adgidzi 2008; Davrieux et al. 2010
Ash (g/100g dw)	1.6-3.2	Adomako 1985; Chukwu & Adgidzi 2008
Minerals (mg/100g dw)		
Ca	0.2-34.1	Megnanou et al. 2007
Na	1.0-9.6	Megnanou et al. 2007
Mg	0.0-8.9	Megnanou et al. 2007
Fe	0.5-6.7	Megnanou et al. 2007
Zn	1.9-3.4	Megnanou et al. 2007
Cu	0.0-1.5	Megnanou et al. 2007
K	0.0-0.4	Megnanou et al. 2007
Mn	0.0-0.14	Alhassan et al. 2011

and is more or less solid at room temperature (Hall et al. 1996). Nutrient and chemical composition of shea butter is illustrated in Table 2.3, where the carbohydrate content of the butter is remarkably high (22.3 g/100g dw) (Chukwu and Adgidzi 2008). Calcium and Sodium were the most abundant minerals in the butter, with mean concentrations of 17.2 and 5.3 mg/100g dw, respectively (Megnanou et al. 2007). Fat content of shea butter across its distribution range varies between 28.0-61.6 % (Kershaw and Hardwick 1981; Davrieux et al. 2010; Gwanli et al. 2012b; Allal et al. 2013), depending on various factors including climatic conditions, genetic variation, age, size, as well as water stress.

Three groups of triglycerides have been identified, namely mono-unsaturated, diunsaturated and polyunsaturated (Kapseu et al. 2001; Di Vincenzo et al. 2005), with Maranz et al. (2004b) reporting 1,3-distearoly-2-oleoyl-glycerol (SOS) and 1-stearoly-2,3-dioleoyl-glycerol (SOO) as the major triglycerides. Sixteen fatty acids have been identified in shea butter (Di Vincenzo et al. 2005) with the main fatty acids reported in Table 2.4. Several authors (Maranz et al. 2004b; Di Vincenzo et al. 2005; Akihisa et al. 2010a; Allal et al. 2013) report that oleic acid is dominant in butters from Eastern Africa, while stearic acid is dominant in samples of West African provenances. While stearic acid is particularly good for use as an industrial base in confectionary and food products (Ming 2008), oleic acid is purposely best as a raw material for cosmetics (Maranz et al. 2004b). The current market prefers butter of the following quality: Free Fatty Acids (FFA) < 7 % and impurities < 1%. Butter quality for the cosmetic industry varies depending on end use, low FFA, white to yellow colour, low water content, low odour, low melting point, and high unsaponifiable fraction (Lovett 2004).

Unsaponifiable matter of shea butter is mainly constituted by triterpene alcohols (α-amyrin, β-amyrin lupeol and butyrospermol) (Alander and Anderson 2002; Akihisa et al. 2010b) with α-amyrin being the most abundant with a mean value of 36.2 % (Akihisa et al. 2010b) while β-amyrin is the least abundant with a mean value of 10.2 % (Peers 1977). The unsaponifiable matters are attributed to anti-inflammatory and antioxidant properties which is one reason that makes shea butter attractive for cosmetic industries (Alander 2004; Maranz and Wiesman 2004). Tocopherol content, which is influenced by climatic factors varies between 13 and 112 μg/g (Maranz and Wiesman 2004; Allal et al. 2013) with α tocopherol being the majority accounting for 64 % (112 μg/g) (Maranz and Wiesman 2004). The quantity of tocopherol type has been used as basis to distinguish between shea from the Eastern and the Western regions of its distribution with γ-tocopherols significantly higher in Eastern than Western shea (Allal et al. 2013). However, Maranz and Wiesmann (2004) posit the amount of α and total tocopherols will increase in shea butter with increasing mean regional temperature. Four sterols have been identified in shea butter namely β-sitosterol, Cholesterol, Δ7-Stigmasterol and stigmasterol (Peers 1977; Njoku et al. 2000). The major phenolic compounds are gallic acid, gallocatechin, epigallocatechin gallate, epigallocatechin, epicatechin and epicatechin gallate (Maranz et al. 2003). Further non-glyceride elements of shea butter consent its use in cosmetic product formulations because the triterpene alcohols of cinnamates possess anti-inflammatory effects, particularly lupeol and α/β-amyrin in their esterified forms (Alander and Andersson 2002; Alander 2004; Akihisa et al. 2010a).

Table 2.4 Fatty acids composition of shea butter (Extracted from: Honfo et al. 2014)

Fatty acid	**Gram fatty acid/100g fat**	**References**
Oleic 18:01	37.2-62.0	Kershaw & Hardwick 1981; Tano-Debrah & Ohta 1994; Tholstrup et al. 1994; Kapseu et al. 2001; Alander & Andersson 2002; Maranz et al. 2004b; Di Vincenzo et al. 2005; Mbaiguinam et al. 2007; Letchamo et al. 2007; Akihisa et al. 2010a; Okullo et al. 2010; Ugese et al. 2010c; Allal et al. 2013; Davrieux et al. 2010; Gwanli et al. 2012b
Stearic 18:00	29.5-55.7	Kershaw & Hardwick 1981; Tano-Debrah & Ohta 1994; Tholstrup et al. 1994; Kapseu et al. 2001; Alander & Andersson 2002; Maranz et al. 2004b; Di Vincenzo et al. 2005; Mbaiguinam et al. 2007; Letchamo et al. 2007; Akihisa et al. 2010a; Okullo et al. 2010; Ugese et al 2010c; Allal et al. 2013; Davrieux et al. 2010; Gwanli et al. 2012b
Linoleic 18:02	4.3-8.9	Mendez & Lope 1991; Tano-Debrah & Ohta 1994; Tholstrup et al. 1994; Kapseu et al. 2001; Alander & Andersson 2002; Maranz et al. 2004b; Di Vincenzo et al. 2005; Mbaiguinam et al. 2007; Letchamo et al. 2007; Akihisa et al. 2010a; Okullo et al. 2010; Ugese et al. 2010c; Davrieux et al. 2010; Gwanli et al. 2012b
Palmitic 16:00	3.3-7.5	Tano-Debrah & Ohta 1994; Tholstrup et al. 1994; Alander & Andersson 2002; Maranz et al. 2004b; Di Vincenzo et al. 2005; Mbaiguinam et al. 2007; Letchamo et al. 2007; Akihisa et al. 2010a; Okullo et al. 2010; Ugese et al. 2010c; Davrieux et al. 2010; Gwanli et al. 2012b
Arachidic 20:00	0.8-1.8	Kapseu et al. 2001; Maranz et al. 2004b; Di Vincenzo et al. 2005; Letchamo et al. 2007; Akihisa et al. 2010a; Okullo et al. 2010; Davrieux et al. 2010; Gwanli et al. 2012b
Linolenic 18:03	0.2-1.7	Tano-Debrah & Ohta 1994; Tholstrup et al. 1994; Akihisa et al. 2010a; Davrieux et al. 2010; Gwanli et al. 2012b
Vaccenic 18:01	0.08-0.90	Davrieux et al. 2010; Gwanli et al. 2012b

2.7 Socioeconomic and rural livelihood empowerment

Shea is an important oleaginous plant that provides unprecedented opportunities to mitigate rural communities’ vulnerability to food insecurity and alleviate rural poverty across the 21 Sub-Saharan countries in which it is distributed. The possible uses of the multi-purpose shea are illustrated in Table 2.5. Generally, the regions within which shea occurs are bereft of poverty and inhabitants are mostly subsistent farmers dependent on rain-fed agriculture. Rainfall is the major determinant of farming patterns in the savanna and the rainy season where land preparation and sowing takes place, is referred to as the hungry season (Maranz et al. 2004a; Pouliot et al. 2008) because the food barns are low or almost exhausted. Shea which bears fruits during the hungry season becomes an important gap-filling environmental tree both as food and sold for cash (Pouliot 2012). Shea is believed to be the main cooking oil for more than 86 million rural people across its range (Naughton et al. 2014) and is also widely regarded as an important melliferous species throughout the savanna zones (Chevalier 1948; Hall et al. 1996).

Table 2.5 Potential uses of shea in industry and local communities

Usage (Part/extract)	Pharmaceutical/Medicinal/Cosmetic	Culinary/Other uses
Butter	Care of sprains (Bonkoungou 1987) Treating wound (Abbiw 1990; Wallace-Bruce 1995; Egunyomi et al.2009) Child birth (Moore 2008) Dermatitis/dermatoses (Bonkoungou 1987) Massage pregnant women/children (Marchand 1988) Skin lotion and moisturizer, hair lotion (Dalziel 1937) Pomade (Marchard 1988; Bonkoungou1987)	Cooking oil (Lamien 1996; Hall et al.1996) Illuminant (Greenwood 1929; Dalziel 1937) Anointing oil in traditional ceremonies (Goreja 2004; Sturges 2008) Waterproofing of mud Houses (Marchand 1988; Boffa et al. 1999) Soap making (Abbiw 1990; Boffa et. 1999)
Leaves	Analgesic for head, stomach ache (Millee 1984) Jaundice (Bonkoungou 1987) Eye drops/care of eyes (Bonkoungou 1887; Abbiw 1990) Malaria (Bonkoungou 1987)	Spituality and Covering the dead (Agbahungba & Depommier 1989) Fish meal (Obirikorang et al. 2015) Source of saponin used for washing (Abbiw 1990)
Bark/Latex	Bleeding gums (Bognounou 1988) Diarrhoea/dysentery (Soladoye et al. 1989) Cure for jaundice (Ampofo 1983) Stomach ulcers (Hall et al. 1996) Eye wash to neutralize venom of cobra (Soladoye et al. 1989) Infusions used to treat leprosy (Dalziel 1937) Used as a bath to facilitate delivery (Abbiw 1990; Soladoye 1989)	Latex is heated mixed with palm oil and used as glue (Hall et al. 1996) Latex used to mend drums (Millee 1984)
Roots	Cough (Bonkoungou 1987) Cure for jaundice (Ampofo 1983; Hall et al. 1996) Stomach ache (Millee 1984) Chronic sores in horses (Dalziel 1937)	Chewing stick (Isawuni 1978)
Wood		Fuelwood and Charcoal (Danziel 1937; Abbiw 1990) Wood work (Dalziel 1937; Abbiw 1990) Local tools (Dalziel 1937; Abbiw 1990; FAO 1988) Construction (Millee 1984; Abbiw 1990)
Presscake/Nut Residue		Soap making(Hall et al. 1996; Boffa et al. 1999) Cooking fuel (Hall et al. 1996) Termite repellent (Dalziel 1937) Animal feed (Hall et al. 1996) Fish meal (Obirikorang et al. 2015) Used as mulch/Fertilizer (FAO 1988) Removal of heavy Metals from water (Eromosele & Otitolaye 1994)
Caterpillers (*Cirina butyrospermi*)		Eaten fried and a rich source of protein (Greenwood 1929; Ruyssen 1957)

The local shea industry is controlled by women who are involved in fruit and nut collection, processing and commercialization (Lovett and Hag 2000a; Maranz et al. 2003; Chalfin 2004; Elias and Carney 2007). Elias (2015) posits women as being more knowledgeable about the shea tree than men. Traditionaly in the past, shea and its products were not sold and was generally a secondary activity for women to farming. During the period of harvest, women picked shea which was stored for processing at their leisure time. Processed shea was principally for household use and meant for gifts and only rarely sold when money was required for abrupt expenses (Ziba and Yameogo 2002). With the emergent prominence of shea, the picking and processing of shea has now become a full time activity for women and part of the proceeds rather used to employ labour for their farms. Reports in Bukina Faso estimated 300,000-400,000 women participating in shea picking and processing in the year 2000 (Harsch 2001). Shea generally contributes between 2.8-66 % of household income (Becker 2001; Schreckenberg 2004; Pouliot 2012). Based on the prices of shea in 2008, an average monthly income of 53-173 USD is attainable per picker and 97-279 USD per butter extractor in Ghana (Hatskevich et al. 2011). Income generated from the shea trade by women is generally used for sustenance and improvements of the household living standards. Shea thus ultimately has the prospects to offer value addition for women and is a vehicle to improve their livelihoods ensuing the promotion of rural development.

Shea is considered sacred in many rural communities and is seen as blessed by God and a symbol of a maternal tree. As a result it is utilized at birth and death thereby occupying a key position in various cultural and religious ceremonies (Hall et al. 1996; Bayala 2002; Goreja 2004; Sturges 2008). In the Dagomba ethnic group of Northern Ghana, where funerals are performed during the rainy season, the wood of shea is mostly used for firewood because of the scarcity of wood and the hard corky dried bark which easily lights up even when freshly cut during the rainy season. The importance of shea to local communities is further manifested by its use in local poetry, song and dance (Fardon 1990; Kuwabong 2004).

2.8 Future research prospects

The future of research on *Vitellaria paradoxa* should hinge on the following themes: towards a better understanding of the phenology relating to fruiting in order to produce a high, fairly predictable annual yield, domestication of shea by reducing the long juvenile phase of growth, and towards the future distribution of the species in the face of global climate change. To maximize the benefits of the shea resource necessitates that processed shea rather than raw nuts are exported to the international markets. Processing entails the establishment of medium to large scale production centers which would not only create jobs but eventually lead to the sustainable development of the shea belt. But, assurance of a fairly constant supply of nuts on a yearly basis is vital and the yearly production potential of shea needs to be scientifically understood and predictable. There is therefore the need for research to understand the biological and ecological basis for productivity parameters of shea. In this regard, research questions should include (1) the role of shea pollinators and the factors that limit these pollinators, (2) the role of soil nutrients and also bushfire in shea fruiting, and (3) the role of rainfall (moisture) during flowering and subsequent fruiting. Overcoming the long juvenile phase of growth is important for the domestication of the wild species and ultimate cultivation in plantations which would lead to higher and reliable productivity of the shea resource. The way forward in over-coming the long juvenile phase of shea lies in improving the grafting methods and the promising in vitro technology. Research in this regards has come a long way and merely a perfection of the techniques are needed, as well as a need to investigate the management of the grafting environment, as the rainy season could be the best season for grafting in terms of curtailing physiological stress. Studies of the eco-physiology of planted/grafted shea seedlings could be a starting point to understand how the species will adapt to climatic variations like increased CO_2 and drought as proposed by climate change projections. This would provide data for improving models to forcast also the future distribution of shea. Much as the fight towards domestication of the wild species continues on several methodological fronts, in the interim there should be research to test the effect of shea-grass/crop competition under current and predicted future levels of CO_2. Ecologists have used stable isotopes to investigate the effects of past climate variability on species and therefore interpret present change in climate. This tool together with dendrochronological research of shea should aid in the accurate prediction of the future distribution of the species. This could also help in matching the age of shea trees with past climate events and production data.

In conclusion, the establishment of a harmonized methodology for determining the distribution, density, chemical and nutritional analysis as well as characterization of country/regional populations is timeously required. Though the results of vegetative propagation are a basis of hope, optimization and perfection of the techniques are needed for the much desirable benefits to be derived for domestication. We propose research into eco-physiology of shea seedlings under current and projected climate scenarios as well as dendrochronology as the way forward. We also propose eco-physiological studies of the phenophases flowering and fruiting.

CHAPTER THREE

3 EFFECTS OF ELEVATED CARBON DIOXIDE AND CLIMATE CHANGE ON BIOMASS AND NUTRITIVE VALUE OF KYASUWA (*CENCHRUS PEDICELLATUS* TRIN.)

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3.1 Summary

Atmospheric carbon dioxide enrichment enhances plant growth and development and may alter the nutritive value of grasses. The objective of this study was to evaluate growth, biomass partitioning and nutritive value of kyasuwa under combinations of atmospheric CO_2 concentrations, watering and fertilization treatments. Plants were grown in two greenhouse chambers; with ambient (aCO_2; 400 ppm) and elevated CO_2 (eCO_2; 950 ppm), two watering and three fertilization regimes. Elevated CO_2 reduced stomatal conductance by 40%, root to shoot ratio by 8%, leaf to stem ratio (L:S) by 3%, protein content by 14% and Acid Detergent Lignin (ADL) by 23% with no significant changes in total biomass and C/N ratio however, slight increases in leaf area (2%) and Acid Detergent Fiber (ADF) by 4%. Higher fertilization resulted in increased biomass parameters only in well-watered plants while; a lower C/N ratio was recorded with higher fertilization. The L:S ratio was decreased with fertilization while ADL was increased at higher fertilization in well-watered plants. Interactive effects were recorded for ADF content and shoot height. Future eCO_2 will be unfavorable to kyasuwa growth making them less competitive with a reduced nutritive value in drought prone and infertile soils.

Keyword: carbon dioxide, climate change, kyasuwa, nutritive value, plant growth

3.2 Introduction

Cenchrus pedicellatus Trin. (formerly called *Pennisetum pedicellatum* Trin., “kyasuwa”), belongs to the Poaceae family and is a C4 grass (SCHMELZER, 1996). It is native to West Africa and was introduced to India from where it has since spread to South East Asia and Northern Australia (SCHMELZER, 1996) where it is invasive and regarded as an environmental weed (QUDDUS et al., 2014). Kyasuwa is tolerant of disturbance with broad climatic amplitude, produces large quantities of seeds with an efficient dispersal mechanism (SCHMELZER, 1996). It occurs along road edges, disturbed and abandoned lands and thrives on soils of a wide pH scale in rainfall regimes ranging between 500-1500 mm with severe drought lasting 4-6 months (FAO, 2010; SCHMELZER, 1996). Kyasuwa provides succulent, palatable and nutritious forage over a long growing season including the dry periods of October-November and contributes to meeting Cattle fodder requirements in rural areas (SCHMELZER, 1996; FAO 2010). It is also used as a soil stabilizer, mulch and in soil erosion control (SCHMELZER, 1996; FAO, 2010).

Climate change is one of the most severe challenges of our time, with predicted increases in global mean temperature, length and severity of drought events and atmospheric CO_2 concentration, due to human activities (IPCC, 2014). Many plants respond to elevated atmospheric carbon dioxide (eCO_2) concentrations by increased growth, biomass and productivity, with C3 plants generally benefitting more than C4 plants (SANTOS et al., 2014; AINSWORTH AND ROGERS, 2007). Moreover, there are also reports of significant changes in the chemical composition of plants under eCO_2 (MYERS et al. 2014). Nonetheless, plant responses to eCO_2 are not easily predictable because they depend on multiple environmental factors which are not necessarily additive (ACKERLY et al., 1992). Water and nitrogen (N) availability are two of the most limiting plant resources and have been reported to interact with eCO_2 (ERBS et al., 2015). Several studies have shown that the photosynthetic capacity of plants grown at eCO_2 will be acclimated and even down-regulated due to feedback repression of accumulated carbohydrates (PAUL AND DRISCOLL, 1997). This has especially been observed when the plant's C/N status is high due to deficient N supply, leading to a decrease in Rubisco activity and thus, lower photosynthetic rates (LEAKEY et al., 2012). Biomass enhancement of eCO_2 may therefore be dependent on sufficient N supply in some species (DONG et al., 2016). In contrast, some species may show enhanced C gain per leaf N due to a suppression of photorespiration under eCO_2 (LEAKEY et al., 2012).

There is a general lack of data on responses of tropical and subtropical plants to future climate changes and more research on plant responses of C3 than C4 species (LEAKEY, 2009). The purpose of this work was to determine the effects of future elevated atmospheric CO_2 concentration on biomass development which aids invasive potential and nutritive value of kyasuwa grass. The objectives of the study were, (1) to assess the effects of eCO_2 on kyasuwa growth, biomass allocation and nutritive value, (2) to evaluate how different water and fertilization regimes affect kyasuwa growth, biomass allocation and nutritive value and, (3) to estimate interactive effects of the three resource factors on these traits of kyasuwa. We hypothesize future increases in atmospheric CO_2 will increase kyasuwa growth and biomass thereby enhancing competitiveness. We also hypothesize that nutritive value of kyasuwa will increase with eCO_2 especially at high fertilization regimes.

3.3 Materials and methods

3.3.1 Plant preparation and growth conditions

Seeds for the study were harvested in January 2016 from 150 plants located in Tolon in the Guinea savanna zone of Ghana (09° 25'N, 00° 58'W). Seeds were transported within 3 weeks of picking to the greenhouse of Universität Hamburg, Germany (53° 30'N, 10° 12'E). Germination and pre-treatment growth were carried out as follows in the greenhouse. After a germination period of 3-6 days in germination trays, two plants were transplanted into a 3 L plastic pots of 15 cm height, filled with a mixture of 4:1:0.5 (v/v) sand (0.13 – 0.36 mm), clay and standard organic substrate (TKS1, Floragard Vertriebs-GmbH, Oldenburg). The bottom of the pots was secured with a weed mat to prevent loss of substrate. After pre-treatment growth for 20 days, the pots were randomly assigned to two growth chambers (each 28.5 m^2) of different CO_2 concentrations in a green-house with controlled growth conditions (Day/night air temperature 25°C/22°C; 70%-80%

relative air humidity; Length of photoperiod same as Hamburg area). We stimulated the atmospheric CO_2 concentration of 950 ppm based on the representative concentration pathway (RCP) 8.5 scenario by 2100 (IPCC, 2014). In the first growth chamber, the CO_2 concentration was the same as in ambient atmospheric air (aCO_2; 400 ppm) while in the other chamber, the CO_2 was elevated to 950 ppm (eCO_2).

Three fertilization treatments were applied using commercial liquid fertilizer with NPK values of 8-8-6 (WUXAL Super, Aglukon Spezialdünger GmbH, Düsseldorf, Germany). The treatments corresponded to the equivalent of 75 kg N ha^{-1} (N-1), 100 kg N ha^{-1} (N-2) and 125 kg N ha^{-1} (N-3) and were applied at planting, 20 days after planting and 40 d after planting. The WUXAL super fertilizer has the full complement of macro and micro nutrients. During the experimental period of 68 days two watering regimes of continuous watering (wet), and a stimulated drought period of no watering (dry) for 2 weeks were implemented. The complete design of the study comprised of two levels of CO_2, two watering regimes, three fertilization regimes and six replicates, resulting in a total of 72 pots for the entire experiment. The pots were equally distributed among the two growth chambers which resulted in 36 pots in each chamber. To avoid edge and chamber effects, the positions of individual potted plants were rotated on the tables on a weekly basis but, it was practically impossible to switch CO_2 concentrations between the two chambers however, the growth conditions were similar. During the experiments, the CO_2 level, temperature and air humidity were monitored by the Computer Climate model CC 600 (RAM co. Measurement and Control, Germany) every 12 minutes. The light conditions in the two chambers were measured for a month with quantum sensors (LI-190R, LI-COR, Lincoln, NE, USA) connected to data loggers (CR 1000, Campbell Scientific, Logan, UT, USA). The grasses were exposed to the experimental treatments for a total of 68 days during the growth period (May-July 2016).

3.3.2 Plant growth and physiological measurements

To assess the effects of eCO_2, watering and fertilization regimes, the growth characteristics were recorded before harvesting the grass 80-90 days after sowing. Shoot height was measured from ground level to the base of the top-most, fully developed leaf or to the base of the panicle depending upon the stage of the particular plant. The stomatal conductance was measured on two leaves for three replicates within all treatments using a leaf porometer (SC-1, Decagon Devices, Pullman, WA, USA) on young but fully developed leaves. At harvest, the area of the individual grass leaves was determined using an area meter (LI 3100, LI-COR, Lincoln, NE, USA) while the fresh weight of leaves and stems were measured separately and the leaf to stem ratio (L:S) estimated from these measurements. Roots were thoroughly washed from the soil over a sieve with 1 mm mesh size. The biomass fractions (leaves, stems and roots) were oven dried for 48 hours at 65°C. Roots were denominated below-ground biomass (BGB). Above-ground biomass (AGB) was estimated by adding dry weights of leaves and stems, while total biomass (TB) was the sum of AGB and BGB. The root to shoot ratio (R:S) was calculated by dividing BGB by AGB.

3.3.3 Forage nutrient analysis

To evaluate the effects of eCO_2, watering and fertilization regimes on nutritive value of kyasuwa, oven-dried leaves and stems were ground separately with a micro hammer mill (Culatti AG, Zürich, Switzerland) fitted with a 1 mm sieve. Neutral detergent fibre (NDF) and acid detergent fibre (ADF) were measured sequentially with the ANKOM filter bag method according to the manufacturer, using a fibre analyzer (ANKOM-200 Fiber Analyzer, ANKOM Technology, Macedon, NY, USA). Ground leaf and stem material (500 mg) was placed in ANKOM F57 filter bags and sealed with heat. All 72 samples were first extracted with neutral detergent, and the residue was weighed to determine percentage of NDF. The NDF residue was then extracted with acid detergent solution, followed by extraction with 72% H_2SO_4 and ashing to determine the percentage of acid detergent lignin (ADL) (VAN SOEST, 1994, RYAN et al., 1990). The following nutrient parameters were estimated: % NDF, % ADF, and % ADL.

Total nitrogen and carbon concentration of leaves was measured in aliquots of oven dried samples by an elemental analyzer following pyrolysis (EURO-EA 3000, Euro Vector, Italy). Mass calibration was conducted by the use of the certified standard 2,5-bis (5-tert-butyl-2-benzoxazol-2-yl) thiophene (6.51% N; 72.52% C; HEKAtech, Germany). The percentage of proteins in leaves was measured according to BRADFORD (1976): Dried leaves of all treatments were finely ground using a Retsch mixer mill (MM-400, Fischer Scientific, Suwanee, USA) and thereafter digested in 0.1 M NaOH for 30 minutes (JONES et al., 1989). A volume of 100 µl aliquots of centrifuged supernatant were assayed with 50 µl

Bio-Rad Bradford dye (Coomasie brilliant blue). Absorbance was measured at 595 nm after 15 minutes using a multi-mode microplate reader (Synergy HT, BioTek Instruments, Winooski, USA).

3.3.4 Data analysis

All statistical analyses were carried out using the software package Statistica 13 (Stat-Soft Inc., Tulsa, OK, USA). Growth, biomass and nutritive value parameters were analyzed by three-way analysis of variance (ANOVA) to test for significant main effects of the factors CO_2 concentration, fertilization levels and watering regime as well as all factor interactions, followed by the Tukey HSD post hoc test of significant differences. For analysis of nutritive value, data of stems and leaves were averaged after chemical assays. Prior to the 3-way ANOVA, all data were analyzed for homoscedasticity using Levene's test, and data were transformed appropriately where necessary. In addition, residual plots and normal probability plots were inspected to ensure that the assumptions of ANOVA were met.

3.4 Results

3.4.1 Environmental conditions during the study

Throughout the experiment, the monitored average daily temperature in both the ambient and elevated CO_2 chambers was 26°C ±1°C. The relative humidity of the ambient CO_2 chamber was 79%±7% while that of the elevated CO_2 chamber was similarly 73%±8 %. The light conditions of the two chambers were similar. Overall, the environmental conditions in two chambers were stable and similar throughout the duration of the study except the ambient CO_2 (400 ppm) and the elevated CO_2 (950 ppm) in the elevated chamber.

3.4.2 Effects of elevated CO_2 on kyasuwa

Kyasuwa grass grew well in the two CO_2 chambers and showed no signs of nutrient deficiencies or pest attacks. Elevated CO_2 significantly reduced stomatal conductance ($p < 0.001$), leaf to stem ratio ($P = 0.04$) and root to shoot ratio ($P = 0.01$) by 40%, 3% and 5%, respectively (Tab. 3.1, Fig. 3.1). However, leaf area ($P = 0.014$) was significantly increased by 2% with increased carbon dioxide concentration (Fig. 3.1, Tab. 3.1). Above-ground and total biomass was not significantly affected by atmospheric CO_2 concentration (Tab. 3.1).

Growth under eCO_2 significantly increased structural carbohydrates (ADF) by 2% ($P < 0.001$). However, ADL and percentage protein were reduced by 23% ($P < 0.001$) and 14% ($P < 0.001$), respectively (Fig. 3.1, Tab. 3.1). The C/N ratio was not significantly affected by CO_2 concentration.

3.4.3 Water and fertilization regime effects on kyasuwa growth and nutritive value

The high-watering level significantly increased by 1% ($P < 0.001$) the ADF content (Fig. 3.1). Increased nutrient availability reduced the leaf to stem ratio by 6% between N-3 and N-1 ($P=0.002$), and by 4% ($P = 0. 04$) between N-2 to N-1 (Tab. 3.1, Fig. 3.1).

Table 3.1. F-values of three-way ANOVA of all measured parameters of kyasuwa grass grown under elevated and ambient CO_2, three fertilization and two watering regimes. n=6

	Sources of Variation						
Parameters	**CO_2 (C)**	**Water (W)**	**Fertilization (N)**	**C*W**	**C*N**	**W*N**	**C*W*N**
Growth & Biomass							
Height (cm)	**10,63****	**47,87*****	0,77	0,58	0,07	1,42	**4,15***
Leaf area (cm^2)	**6,37****	0,03	0,44	0,00	0,18	0,64	0,33
Stomatal conductance (mmol mol^{-1})	**7,30****	0,73	0,13	2,54	0,23	0,73	1,03
Leaf to stem ratio	**4,62***	2,49	**7,04****	0,10	2,06	0,06	0,60
Root to shoot ratio	**7,09****	2,41	0,46	0,09	0,17	0,23	0,09
Above ground biomass (g)	0,00	**63,52*****	**9,67*****	1,32	2,59	**7,02*****	2,56
Below ground biomass (g)	**9,30****	**36,69*****	**9,95*****	3,11	2,12	**4,90****	2,81
Total biomass(g)	0,71	**54,04*****	**10,10*****	1,26	2,26	**5,68****	2,75
Nutritive value							
C/N ratio	0,59	**53,98*****	**11,60*****	1,64	0,39	**5,88****	1,22
% Protein	**30,38*****	1,17	0,46	0,44	0,44	0,72	1,31
% Neutral detergent Fibre	**23,45*****	1,42	2,36	1,03	**5,31****	2,34	0,55
% Acid detergent Fibre	**111,34*****	**16,61*****	1,79	0,00	1,44	0,82	0,23
% Acid detergent lignin	**14,38*****	2,06	0,78	3,87	1,64	**3,23***	0,30

Statistically significant values in bold; * <0,05, **<0,01, ***<0,001 probability levels

We found significant interactions between watering and fertilization regimes for AGB, BGB and, TB (P= 0.02; 0.01; and 0.005; respectively) (Fig. 3.2a). Increasing fertilization caused significant increases in these three biomass parameters but only with concurrently high water availability. At low water availability, no biomass responses to fertilization regime could be detected.

For nutritive components, we observed two way interactions of watering and fertilization regimes for the C/N ratio (P= 0.005) and ADL (P= 0.046) (Fig. 3.2b, c). The C/N ratio was lowered with higher levels of fertilization, but only in drought-exposed plants. The ADL concentration was higher at the highest than the two lower fertilization levels, but only in well-watered plants.

3.4.4 Interactive effects of elevated CO_2 with fertilization and/or watering regimes

There was a two-way interaction between carbon dioxide enrichment and fertilization regime for NDF (P= 0.008; Tab. 3.1; Fig. 3.3a). Here, eCO_2 had no effect on NDF at the low fertilization level, while it resulted in increased NDF at the higher nutrient availability N-3 (Fig. 3.3a). A significant three-way interaction (P= 0.02) of CO_2 concentration, water and fertilization regimes was observed for shoot height (Fig. 3.3b). Under aCO_2, the higher fertilization regimes (N-2 and N-3) increased shoot height in well-watered plants but decreased shoot height in drought-treated plants. However, under eCO_2, higher fertilization regimes (N-2) resulted in increased shoot height at lower water regimes, but well-watered plants had taller shoots than drought-treated plants though no fertilization effects were recorded.

3.5 Discussion

3.5.1 Growth and biomass

Most plants, both C3 and C4, respond to eCO_2 by reducing stomatal conductance (AINSWORTH AND ROGERS, 2007; AINSWORTH AND LONG, 2005). In the present study, kyasuwa responded to eCO_2 by reducing its stomatal conductance (g_s), which usually translates into reduced water loss through lower transpiration rates and higher water use efficiency at the leaf level (EAMUS et al., 2008). A review of the effect of eCO_2 on both C3 and C4 vegetables pointed to down-regulating of stomatal conductance and lowering of transpiration, the combination of which leads to higher water use efficiency (BISBIS et al. 2018).

There are several studies showing that both tropical and temperate C4 grasses benefit from eCO_2 by down-regulating their stomatal conductance and thus, water loss, rather than increasing their above ground and or total biomass (XU et al., 2014; KAKANI AND REDDY, 2007). Except shoot height, we did not find any interaction of watering regime and atmospheric CO_2 concentration on any other investigated parameters, so it is unlikely that eCO_2 had any effects on the integrated water-use efficiency of kyasuwa, although g_s was lower under eCO_2, which at first sight might be indicative of an increased instantaneous water-use efficiency. In the case of shoot height there was a three-way interaction with differences recorded in the low water treatments of aCO_2 and eCO_2 in higher fertilization regimes. Since consequently the net CO_2 flux into the leaves might have been the same at both high and ambient CO_2 concentrations, irrespective of the water availability, the lower stomatal conductivity in eCO_2 was the result of an adjustment of the CO_2 influx to an apparently unchanged CO_2 demand reflecting a similar assimilation potential under both atmospheric CO_2 conditions (GHANNOUM et al., 2000). This suggestion is further supported by similar C/N ratios at aCO_2 and eCO_2.

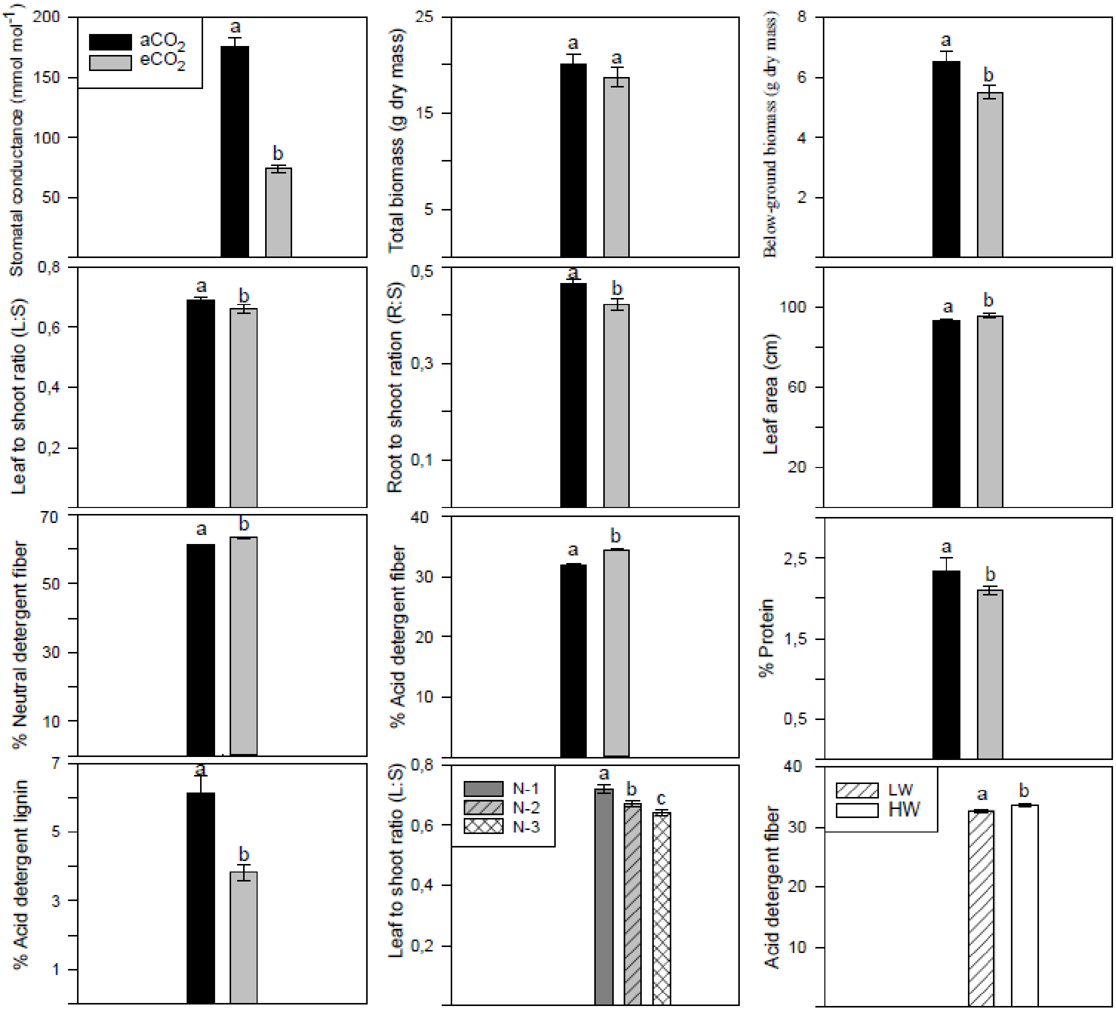

Fig. 3.1: Main effects of CO_2 concentrations, watering and fertilization regimes on growth, biomass parameters and nutritive values of kyasuwa. Different lowercase letters represent significant differences among treatments. LSM ± SE. eCO_2, elevated CO_2 concentration; aCO_2, ambient CO_2 concentration; LW, Low water treatments; HW, High water treatment; N-3, High fertilization regime; N-2, medium fertilization regime; N-1, low fertilization regime.

The effects of eCO_2 on kyasuwa growth and biomass seemed to be confined to changes in biomass allocation patterns in the present study. The decrease in the root to shoot ratio and the general reduction in below-ground biomass with eCO_2 has previously been observed (KAKANI AND REDDY, 2007). The effect of eCO_2 on R:S is mechanistically not well understood, but it varies with plant types and resource supply (ROGERS et al., 1996). Other studies have both found an increase (ARNONE et al., 2000) and no change in R:S (KÖRNER et al., 1997). As a general principle of allocation, under changing resource availability (light, water, nutrients, CO_2), plants tend to enhance organs that can increase the capture of the resource that is becoming limiting, partly to the detriment of other organs. In our study, as in others, increased CO_2 supply caused lower stomatal conductivity leading to reduced water demand. Consistent with the above-mentioned principle, the allocation to root growth has been reduced, whilst a significant increase in leaf area as a response to eCO_2 has been observed which is also reported in other studies (ACKERLY et al., 1992). By lowering investment in below-ground biomass, the plant's rooted soil volume is reduced and, thus, not only less nutrients but also less soil water is available to the plant. Consequently under eCO_2 shorter dry spells could be withstood devoid of severe distress. However, kyasuwa will be more susceptible to extended drought because less soil volume will be used for water uptake and thus less competitive in the drier savanna.

The observed decrease in leaf to stem ratio (L:S) signifies that eCO_2 resulted in higher allocation of biomass to stems, which has been previously reported in other C4 grasses (SANTOS et al., 2014). On one hand, if the lower L:S ratio is combined with the increased leaf area, plants grown at eCO_2 developed overall broader leaves and denser shoots than those grown at aCO_2, which is beneficial for future use of the species, as livestock prefer leaves with broader blades (BATISTOTI et al., 2012). On the other hand, a high leaf to stem ratio is generally preferred as an important factor in diet selection, quality and forage intake (SMART et al., 2004).

However, L:S was significantly reduced with higher fertilization regimes because of higher accumulation of stems as reported by other studies (SALVADOR et al., 2016).

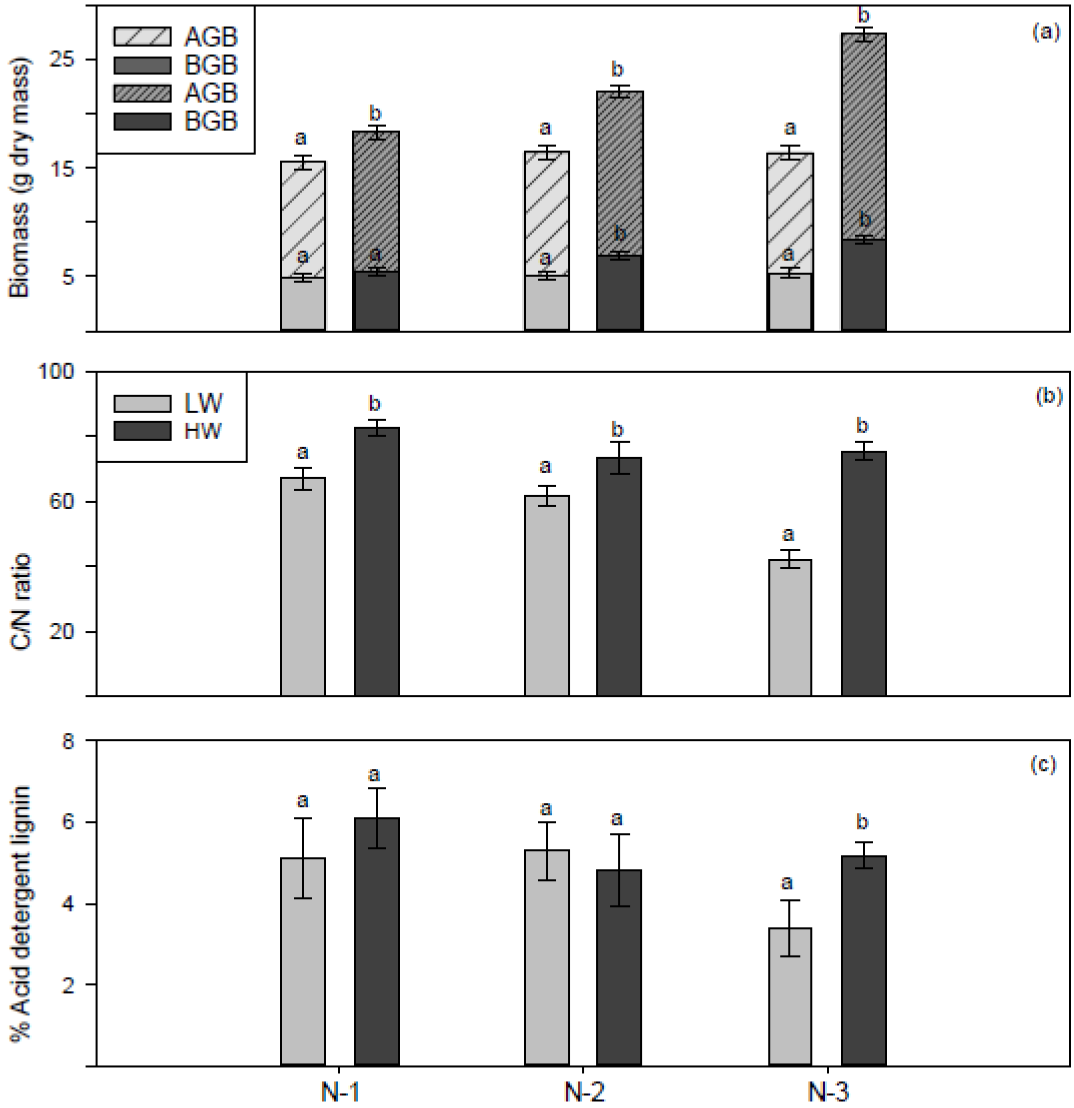

Fig. 3.2: Two-way interactions between watering and fertilization regimes on biomass of kyasuwa (a). Interactive effects of fertilization and watering regimes on nutritive value parameters of kyasuwa (b, c). Different lowercase letters represent significant differences among treatments. LSM ± SE.

Water availability is one of the main biophysical limitations of grass growth in savannas (DEL GROSSO et al., 2008). Water in general is one of the most important limiting resources to plant growth, and in the present study, low soil water content decreased all the biomass parameters as well as grass shoot height. Water deficiency decreases transpiration rate via decreased stomatal conductance, which results in a decline of net photosynthetic rates (FLEXAS AND MEDRANO, 2002). Although C4 species have inherently lower stomatal conductance than C3 and thus have higher water use efficiency, they can still be threatened by drought. In the present study, it is more likely that the effects of water availability on growth were displayed through indirect effects for example lower mobility of nutrients in dry soil rather than a direct effect via stomatal conductance, which did not respond to watering regime. The water by fertilization regime interactions for kyasuwa showed that water supply was the main limiting factor for biomass accumulation and height growth. Water availability is pivotal for increasing nutrient availability for kyasuwa growth and biomass production, and elevated CO_2 did not help to improve the water use efficiency of this species. However, some plants do not reduce water loss through stomata closure but, react to water shortage by investing assimilates into protective substances (i.e. synthesis of LEA-proteins and other osmoprotectants, compatible solutes etc) and consequently they have a lower biomass under drought treatment (SCHULZE et al., 2005).

3.5.2 Kyasuwa tissue nutritive value

The significant reduction of the protein content under eCO_2 has been attributed more to a dilution-effect due to an overall increase in total non-structural carbohydrates, rather than an absolute decrease of the protein content in leaves (DUMONT et al., 2015). This is unlikely to be the case in the present study, since the C/N ratio was unaffected by CO_2 treatment. Other studies implicate the decrease in Rubisco concentration (AINSWORTH AND LONG, 2005) due probably to carbohydrate-dependent decrease in expression of photosynthetic genes (MOORE et al., 1999) and decreased transpiration and stomatal conductance (DEL POZO et al., 2007). A meta-analysis on proteins in food crops also indicates a reduction of proteins at elevated CO_2 (TAUB et al., 2008). We suggest that a re-allocation of N to resources other than proteins occurred within kyasuwa, for example to structural N-compounds or free amino acids or even to vacuolar nitrates, leaving a similar C/N ratio in the aCO_2 and eCO_2 treatment. The lack of effect of eCO_2 on the C/N ratio could be a result of C4 plants photosynthesis and biomass accumulation being less affected by eCO_2 (WANG et al., 2012). C4 plants are less affected by eCO_2 because of their C-accumulation strategy, which minimizes photorespiration through anatomical and biochemical specializations that concentrate CO_2 at the active site of Rubisco (SAGE, 2004) and are virtually CO_2 saturated already at aCO_2.

Low soil water potential generally impairs plant metabolism and there are suggestions that water availability plays a key role in nutrient limitations to grasses of semi-arid areas (LÜ et al., 2012). This is because of the vital role water plays in nutrient transport and availability for nutrient uptake in plant roots. The interactive effect of watering and fertilization regimes on C/N ratios showed higher fertilization regimes reducing C/N ratios when water availability was limiting. Several studies support the finding of an interaction between water availability and nitrogen nutrition for C/N ratio (LÜ et al., 2012). In nature, soil water availability influences soil N availability via many microbial aided pathways like litter decomposition (Liu et al., 2006) and N mineralization (Wang et al., 2006). In the present study, the high water availability probably had a direct effect on nutrient availability to plant roots by increasing their diffusion and mass flow in the soil. The lower C/N ratio may therefore be an expression for a relative decrease in C-assimilation rates under dry conditions when nutrient supply was high.

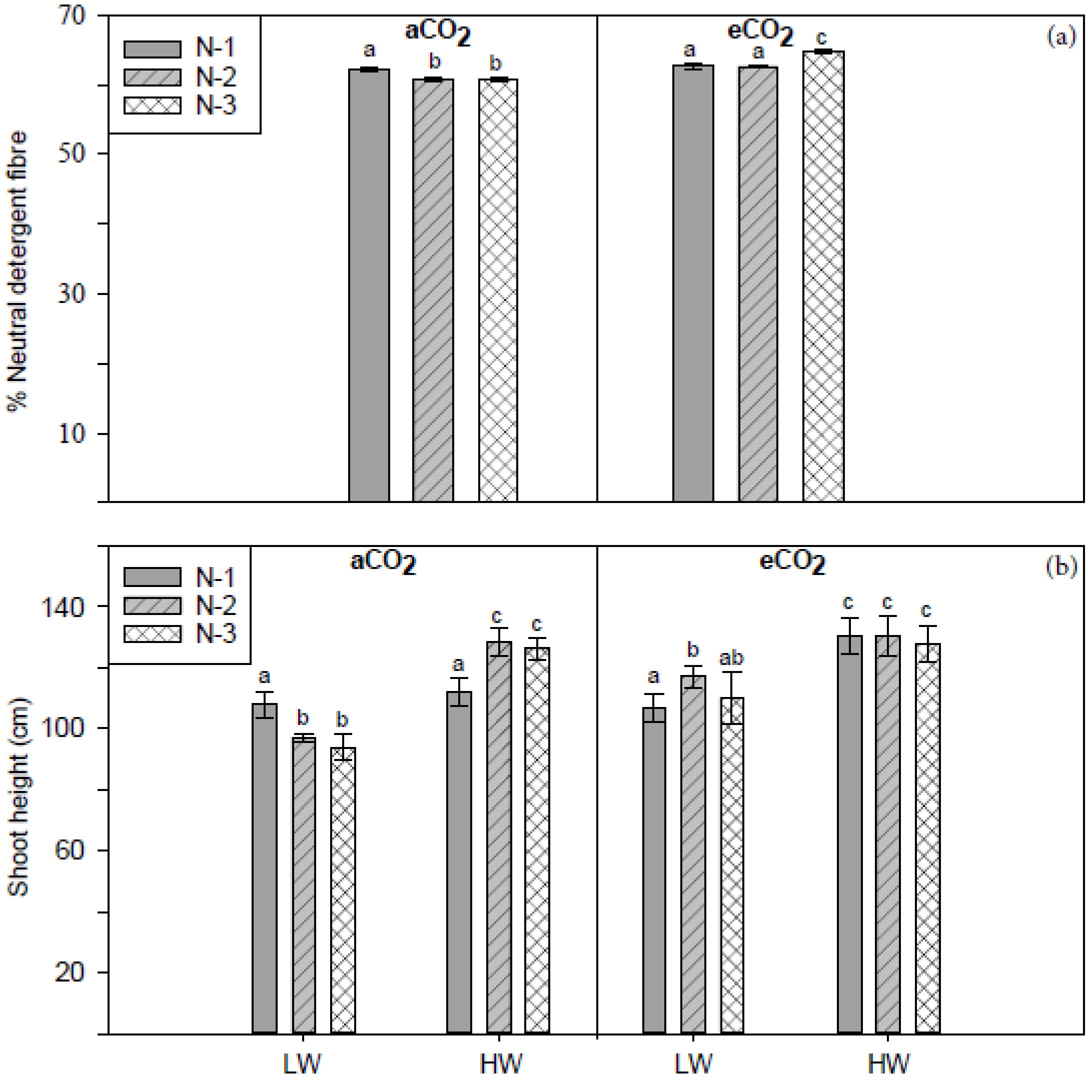

Fig. 3.3: Two-way interaction of CO_2 concentrations and fertilization regimes on neutral detergent fibre of kyasuwa (a) and three-way interaction between CO_2 concentrations, watering and fertilization regimes on kyasuwa shoot height (b). Different lowercase letters represent significant differences among treatments. LSM ± SE.

NDF concentration was increased at high fertilization regimes only under eCO_2, which is in concert with previous observations of soil N supply limiting the ability of plants to respond to eCO_2 (DONG et al., 2016). Plants with low N-demand, however, may respond to eCO_2 even in N-poor soils (NORBY et al., 1992). The present study showed that the main effects of eCO_2 on NDF were significant but rather small, as reported by other studies (FRITSCHII et al., 1999; AKIN et al. 1995), and therefore future atmospheric CO_2 concentration can be expected to increase fiber content of kyasuwa to a minimal extent, and only if a high fertilization load is provided.

ADF concentration was significantly reduced by drought, which may have been caused by delayed plant maturity due to stressful arid growth conditions (KÜCHENMEISTER et al., 2013). Plant fibre contents turn to increase with age since the stem to leaf ratio increases with age, and fiber content of stems is considerably higher than leaves (BRUINENBERG et al., 2002). The increases in structural carbohydrates with eCO_2 recorded in this study have previously been observed and seem to be species-dependent (DUMONT et al., 2015; MILCHUNAS et al., 2005; FRITSCHI et al., 1999; AKIN et al., 1995). In wheat for instance, AKIN et al. (1995) recorded increased contents in fibre fractions with eCO_2, while FRITSCHI et al. (1999) reported increases in structural carbohydrates of *Arachis glabrata* leaves. MILCHUNAS et al. (2005) likewise recorded increases in combined cellulose and hemicellulose in *Bouteloua gracilis* with eCO_2. However, a recent meta-analysis of forage quality of Mediterranean grasslands pinpointed no change in structural carbohydrates with eCO_2 (DUMONT et al., 2015).

ADL concentration was increased at the highest fertilization level, but only in well-watered plants, which could be the result of lower L:S ratio with higher fertilization regimes. Moreover, ADL was lowered by eCO_2, which means that the tissue quality as forage can be expected to be higher under future eCO_2 concentrations. The reducing effect of eCO_2 on lignin components of forages has been reported in previous studies (MILCHUNAS et al., 2005; AKIN et al. 1995) which may be caused by lignin being connected chemically to proteins and carbohydrates in the cell wall to form large macromolecules (MOORE AND JUNG, 2001). A higher NDF concentration reduces animal intake while a higher ADF concentration decreases digestibility (SAHA et al., 2013). However, decreases in ADL increases digestibility because lignin limits digestion (MOORE AND JUNG, 2001). We therefore propose that the overall quality of kyasuwa as forage will be lower under eCO_2. Vegetables are reported to increase in sugars, vitamin C, phenols, flavonoids and antioxidant capacity as a result of eCO_2, however the macro and micronutrients are reduced (BISBIS et al. 2018).

3.6 Conclusion

Elevated CO_2 increased individual leaf area of kyasuwa which would make the grass attractive as forage. However, eCO_2 resulted in a change in biomass allocation towards a lower R:S ratio, that ultimately may be harmful for the species especially under dry conditions and low nutrient availability making it less competitive. Moreover, eCO_2 will result in changes in the chemical composition of kyasuwa with increases in structural carbohydrates (NDF and ADF) and reduction in ADL and protein which will reduce the nutritive value of kyasuwa overall. Water and fertilization were the two most limiting resources for kyasuwa compared to CO_2 and did not interact with CO_2 except in shoot height and NDF. As a compromise for future tissue quality, we suggest to avoid over-fertilization of kyasuwa to avoid an undesirable increase in fibre content.

3.7 Acknowledgement

The authors are grateful to Prof. Dr. Jörg Fromm and the Institute of Wood Science/vTI Hamburg for allowing us to use their greenhouse. We also wish to thank Prof. Dr. Jörg Ganzhorn of Animal Ecology and Conservation, University of Hamburg for allowing us to use their Fiber Analyzer for nutrient analysis.

CHAPTER FOUR

4 ELEVATED CO_2 DOES NOT OFFSET EFFECTS OF COMPETITION AND DROUGHT ON GROWTH OF SHEA (*VITELLARIA PARADOXA* C.F. GAERTN.) SEEDLINGS

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4.1 Abstract

The shea tree (*Vitellaria paradoxa* C. F. Gaertn.) is a major parkland species occurring across Africa from East to West. Its fruits, butter, and further products from shea butter play key roles in the Sustainable Development Goals of poverty eradication, hunger elimination, and gender equity in many African regions. The inter-play of abiotic conditions (e.g. rainfall patterns, drought periods) and biotic interactions (grazing by large herbivores) shape parklands because they influence vital processes like photosynthesis, transpiration and biomass production of common plant species including shea. We measured gas exchange of shea seedlings grown under ambient and elevated atmospheric CO_2 (eCO_2), with and without competition of the C4 grass *Cenchrus pedicellatus*, and under different water availabilities in greenhouse chambers. We hypothesized that eCO_2 will generally increase seedling growth in shea via increases in photosynthesis. When growing together with C4 grass at low water availability, we expect an improved competitiveness of shea under eCO_2, beacuse eCO_2 is reported to augment water use efficiency (WUEi) of C3 plants more than C4 plants. Increased CO_2 caused a 10% ($p<0.001$) increase in maximum light-saturated photosynthesis (*A*max), 22% ($p<0.001$) increase in WUEi and 13% ($p<0.001$) increase in stem mass fraction (SMF) of shea. Grass competition significantly reduced *A*max by 9% ($p<0.001$), SMF ($p<0.001$) by 19%, with a corresponding reduction in all biomass parameters, but also significantly increased the C/N ratio (by 3%, $p<0.001$). Interactive effects of eCO_2 and competition were recorded for maximum electron transport rate, dark respiration, stomatal conductance, CO_2 compensation point and the leaf area ratio. The control of grasses in the early stages of shea development is therefore recommended.

Keywords: Biomass, competition, CO_2, photosynthesis, shea, water use efficiency.

4.2 Introduction

The shea tree (*Vitellaria paradoxa* C. F. Gaertn.) is a major species in parklands which constitute the most wide-spread ecosystem in arid Africa (Boffa 2015). Parklands are savanna landscapes in which mature trees occur scattered in cultivated or recently fallowed fields (Pullan 1974; Bonkoungou et al. 1994; Boffa 1999).The species is native to the savanna belt of the Sudanian region centre of endemism from Senegal to the foothills of the Ethiopian highlands (White 1983) across 21 countries (Boffa 2015; Naughton et al. 2015) covering a belt of 6,000 km long (Okullo et al. 2004; Sanou et al. 2006). Shea trees and their products can contribute substantially to three important 2015-2030 United Nation's Sustainable Development Goals (SDGs) of poverty eradication, hunger elimination, and gender equity through women empowerment (Naughton 2016). Recent reviews on shea have detailed the chemical and nutritional properties (Honfo et al. 2014), opportunities and challenges for improvements (Boffa 2015) and current knowledge and research gaps (Tom-Dery et al. 2017).

A distinctive ecological feature of savannas is the co-existence of grasses and trees (Scholes and Archer 1997). The tree–grass interactions in savannas have been investigated with regards to competition for water and nutrients (Scholes and Archer 1997; Jeltsch et al. 2000; House et al. 2003; Sankaran et al. 2005), disturbance regimes like fire (Jeltsch et al. 2000; Higgins et al. 2000; Van Langevelde et al. 2003; Bond et al. 2003; Sankaran et al. 2005), mammalian herbivory (Van Langevelde et al. 2003; Sankaran et al. 2005) and demographic bottlenecks to tree recruitment (Jeltsch et al. 2000; Higgins et al. 2000; Midgley and Bond 2001; Riginos 2009; Vadigi and Ward 2013). Grasses are reported to intensely compete with trees at various demographic stages (Riginos 2009). However, their effects are most severe at the tree seedling stage when grasses can limit the ability of trees to recruit into saplings and more established size classes, particularly by competition for light and nutrients (Davis et al. 1999; Higgins et al. 2000; Midgley and Bond 2001; Vadigi and Ward 2013). Previous research on biotic interactions of shea trees with other plant species mainly focused on interactions with food crops in agroforestry systems reporting positive effects of bi-cropping on soil fertility and or micro-climate and negative effects of shea shading on crop yield (Bayala et al. 2002, 2008b, 2015; Bazié et al. 2012; Boffa 2015). However, Baziari et al. (2017) reported no direct shading effect of shea trees on crops, but higher soil moisture of the shaded area leading to higher crop yield.

The global climate is predicted to change with increases in mean temperature, length and severity of drought events and atmospheric CO_2 concentration, due to anthropogenic activities (Hartmann et al. 2013; IPCC 2014). In many studies plants respond to elevated atmospheric carbon dioxide concentrations (eCO_2) by increased growth and biomass accumulation (Drake et al. 1997; Wand et al. 1999; Ainsworth and Long 2004). It has also been reported that photosynthetic capacity of plants grown at eCO_2 in pots over long-periods has acclimated and even down-regulated due to feedback repression of accumulated carbohydrates (Arp 1991; Paul and Driscoll 1997). A conspicuous observation in such plants is the increased C/N ratio due to faster N depletion of the soil as consequence of increased growth rates. N limitation can lead to a decrease in Rubisco activity and thus, lower photosynthesis rates (Leakey et al. 2012). Another common response of plants grown at eCO_2 is a reduction of stomatal conductance, which leads to an increased C-uptake per transpired H_2O (water use efficiency, WUE) (Leakey et al. 2012). These general findings give rise to the assumption that plants that benefit most from eCO_2 in terms of growth and fitness might be those, which occur in water-limited environments, and those with ample nutrient supply.

Although much research on the shea species has been conducted, there is very little information on the physiological ecology of shea (Bayala et al. 2008a; Tom-Dery et al. 2017) except for sap flow (Bayala et al. 2008a; Awessou et al. 2017; Bazié et al. 2017), and the effects of water availability on seedling traits (Bayala et al. 2009; Glèlè Kakaï et al. 2011). Currently, the gas exchange of shea and its acclimation plasticity to changing environmental factors are not available. Respective knowledge is pivotal for predicting the relevance of climate change for the future of shea dominated parklands, where C3 trees co-exist with mainly C4 grasses such as *Cenchrus pedicellatus*. Since it is assumed that the competitiveness of C4 plants relative to C3 plants is generally reduced at eCO_2 (Ainsworth and Long 2004; Saintilan and Rogers 2015) particularly under dry conditions, the interaction between the grass and the tree could be affected by climate change.

The main objective of this experiment was to assess the extent to which performance of shea seedlings (in terms of growth and biomass production) would be affected by increases in atmospheric concentrations of CO_2, and how the effects of eCO_2 on shea would be modulated by competition with the C4 grass *Cenchrus pedicellatus* and by water availability. Under ambient CO_2 and without grass competition, we expected a decrease in shea performance under low water availability. To investigate the relevance of possible interaction effects, we conducted a pot experiment using a complete block design with the factors water availability (high and low), grass competition (+/-) and CO_2-concentration (400 ppm = ambient CO_2, 950 ppm = elevated CO_2). Under ambient CO_2, we expect that the decrease in shea performance under low water availability becomes more pronounced under competition, since water resources will be even scarcer. Under elevated CO_2, we hypothesized that lowered stomatal conductivity at unchanged or even higher assimilation potential results in a higher water use efficiency of the C3 plant shea. As a consequence we expect an improved competitiveness against the C4 grass, since plants using the CO_2 concentrating C4 metabolism are reported to be less positively affected by eCO_2 than C3 plants regarding both assimilation potential and WUE. However, where plants grow under water sufficiency, there will be enough water available for shea seedlings even with grass competition and therefore better performance of shea under eCO_2 is expected. Overall, we expect eCO_2 to increase shea performance significantly especially when competing with C4 grasses under low water availability (Fig. 4.1).

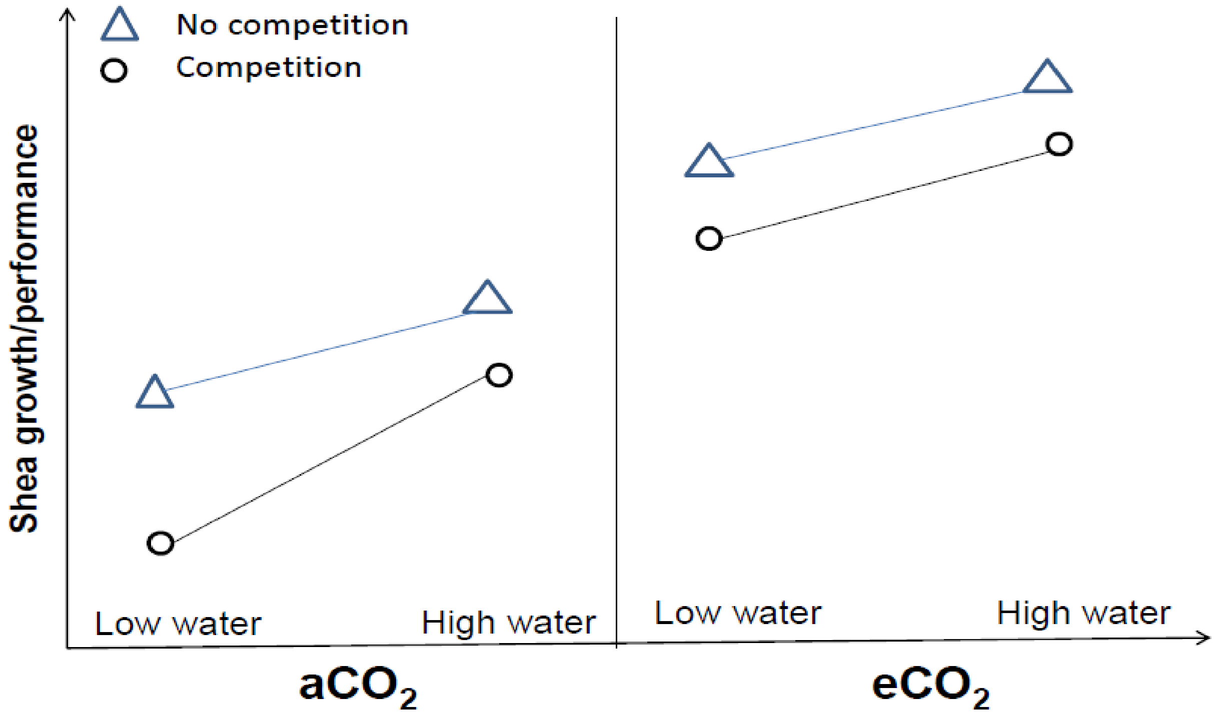

Fig. 4.1 Conceptual model of shea responses to elevated CO_2, grown at low and high water availability and with or without competition.

4.2 Materials and methods

4.2.1 Plant preparation and growth conditions

Shea seeds for the study were picked from 20 trees located in Tolon (09° 25'N and 00° 58'W) in the Guinea savanna zone of Ghana. Seeds were transported within one week to the greenhouse of the University of Hamburg (53° 30'N and 10° 12'E) where they were germinated in trays. The pre-germination lasted for a period of 6 days. This was followed by transfer into 7L plastic pots of 21cm height filled with a mixture of 2:1 (w/w) fine sand (10-20mm) and standard potting substrate (TKS1, Floragard Vertriebs-Gmbh, Oldenburg). The bottom of the pots was tightened with a plastic mesh to prevent loss of substrate during watering. It took a total of eight weeks to complete the germination process. To ensure adequate nutrient availability also under eCO_2, all plants were fertilized with 50 mg N per pot of commercial liquid fertilizer with NPK values of 8-8-6 (WUXAL Super, Aglukon Spezialdünger GmbH, Düsseldorf, Germany). This was the equivalent of 25 Kg N ha^{-1}. WUXAL super fertilizer contains the full complement of macro and micro-nutrients.

After pre-treatment growth for 39 weeks, the pots were randomly assigned to two growth chambers (each 28.5 m^2) of different CO_2 concentrations in a greenhouse with controlled growth conditions (Day/night air temperature 25°C/22°C; 70-80% relative air humidity; Length of photoperiod same as Hamburg area). In the first growth chamber, the CO_2 concentration was the same as in ambient atmospheric air (aCO_2; 400 ppm) while in the other chamber, CO_2 was elevated to 950 ppm (eCO_2). Prior to the experimental period, grass seeds (*Cenchrus pedicellatus* Trin. ‘Kyasuwa’ gathered from the same area as the shea seeds) were nursed for a week in germination trays and three seedlings planted into pots with the shea seedling for competition treatments, while shea seedlings grew alone in the treatments without competition. The quantity of water applied was calculated based on the soil water content at field capacity defined as the soil moisture content when gravity drainage is close to zero after saturation (Ward and Robinson 2000). This was estimated in practice as the amount of water withheld in the soil. Ten pots of substrate dried at 60°C for 72 h were weighed (W1). The pots of dried substrate were thoroughly watered and allowed to drain for 48 h before the pots were re-weighed (W2) and the difference W2-W1 was the quantity of water added to get to 100% field capacity. At field capacity, the soil water content was 1.95 ± 0.33 (w/w). During the experimental period of 16 weeks, two watering regimes of watering at 100% soil field capacity (HW, High water), and watering at 75% of soil field capacity (LW, low water) were implemented on a weekly basis.

A complete block design with seven replicates was comprised of two levels of CO_2, two watering regimes and two competition regimes, resulting in a total of 56 pots for the entire experiment. The pots were equally distributed among the two growth chambers which resulted in 28 pots in each chamber. To avoid edge and chamber effects, the positions of pots were rotated within the chamber on a weekly basis. Due to technical constraints, it was not possible to switch CO_2 concentrations between the two chambers. However, the growth conditions in terms of temperature and air humidity were similar within the two chambers as they were controlled and monitored simultaneously in the two chambers by the Computer Climate model CC 600 (RAM co. Measurement and Control, Germany). Similar light conditions in the two chambers were confirmed by measurements over one month using quantum sensors (LI-190R, LI-COR, Lincoln, NE, USA). The shea seedlings were exposed to the experimental treatments for a total of 16 weeks from May to September, 2016.

4.2.2 Gas exchange and physiological measurements

To better elucidate the underlying processes responsible for differences in shea performance, we measured ecophysiological parameters of shea seedlings. After 16 weeks of growth under experimental conditions, leaf gas exchange was measured using LI-6400XT infrared gas analyzers (IRGA) (LI-COR Biosciences, Inc., Lincoln, NE, USA) equipped with a 6400-01CO_2 mixer and a red-blue 6400-02B LED light source. The second or third fully developed young leaf on the shea shoot that developed during the experimental treatments was measured of four to five replicates of shea seedlings.

The leaf chamber was allowed to acclimatize to the growth chamber temperatures and set on a tripod to ensure stability during the measurements. Readings were taken at air-flow rate of 300 µmol s^{-1} between 10:00 and 15:00 GMT. The CO_2 mixer, containing CO_2 cartridge was installed to ensure a stability of reference CO_2. Before logging, leaves were conditioned to leaf chamber for 10 min at the respective chamber growth CO_2 concentrations and at a PPFD of 1500 µmol$m^{-2}s^{-1}$, until a stable assimilation rate was reached. A/Ci curves (net CO_2 assimilation rate, An, against substomatal CO_2 concentration, Ci) were auto-logged with a minimum waiting time of 80 s and maximum waiting time of 180 s at each CO_2 concentration step. Photosynthetic rates were measured at; 50, 100, 200, 300, 400, 500, 600, 800, 1000, 1200 and at 1500 ppm CO_2, starting with 400 ppm and decreasing CO_2 concentrations till the least and thereafter continuing from 400 ppm again increasing to the highest CO_2 concentration. This pattern was used to prevent the deactivation of enzymes at low CO_2 and avoid the induction of stomata closure at high CO_2. The maximum carboxylation rates of Rubisco (*V*cmax), estimated by Rubisco carboxylation-limited assimilation rate (Ac), and the maximum electron transport rates (*J*max), predicted by RuBP regeneration limited assimilation rate (Aj), were estimated from the A/Ci curves using a curve fitting utility 2.0 (Sharkey et al. 2007; Sharkey 2016) based on the photosynthetic model of (Farquhar et al. 1980; Dubois et al. 2007). The CO_2 compensation (Γ) point was calculated by linear regression from the linear part of the curve below 200 ppm Ci.

The light response curves were auto-logged at the respective growth CO_2 (400 and 950 ppm) with a minimum waiting time of 120 s and a maximum waiting time of 200 s at each step of light intensity. Photosynthetic rates were recorded in a descending order at a PPFD of 1800, 1500, 1200, 800, 500, 250, 100, 80, 50, 20, 0 µmol $m^{-2}s^{-1}$. The dark respiration (R_d), maximum light-saturated rate of photosynthesis (A_{max}), apparent quantum yield (ϕ) and the light compensation point (I_c) were estimated by curve fitting following the model of Buckley and Diaz-Espejo (2015). Stomatal conductance (g_s) and transpiration rate (E) were simultaneously measured with the light response curves and the intrinsic water use efficiency (WUE_i) was calculated by dividing A_{sat} by g_s.

4.2.3 Plant growth and biomass parameters

Leaf area was recorded before harvesting the plants. All leaves from every replicate plant were digitized with a camera (Panasonic DMC-FZ38) and the leaf area was determined with the software Image J (Abramoff et al. 2004). After harvesting, plants were separated into leaves, stems and roots. The roots were thoroughly washed from the soil through a sieve with 1 mm mesh size. Roots were scanned with a desktop scanner (Epson expression 1680) and total root length was determined with Image J (Abramoff et al. 2004; Costa et al. 2014). The collected roots were oven dried (65°C; 48 hours) and weighed as below ground biomass (BGB). Above ground biomass (AGB) was estimated by adding dried weights of leaves and stems, while total biomass (TB) was the total of AGB and BGB. The root to shoot ratio (R:S) was calculated by dividing BGB by AGB.

Seedling traits were estimated as: leaf mass fraction (LMF; total leaf mass divided by TB, g g^{-1}), specific leaf area (SLA, leaf area per leaf mass, cm^2 g^{-1}), leaf area ratio (LAR, total leaf area divided by TB, cm^2 g^{-1}), leaf mass per area (LMA, g cm^{-2}), stem mass fraction (SMF, stem mass divided by TB, g g^{-1}), root mass fraction (RMF, root mass divided by TB, g g^{-1}), specific root length (SRL, total root length divided by BGB, cm g^{-1}) and root length per unit plant mass (RLPM, total root length divided by TB, cm g^{-1}).

4.2.4 C-N analysis

Dried shea leaves of all treatments were finely ground using a Retsch mixer mill (MM-400, Fischer Scientific, Suwanee, USA). Total nitrogen and carbon content of leaves were measured in aliquots of oven dried samples by an elemental analyzer following pyrolysis (EURO-EA 3000, Euro Vector, Italy). Mass calibration was conducted by the use of the certified standard 2,5-bis (5-tert-butyl-2-benzoxazol-2-yl) thiophene (6.51% N; 72.52% C; HEKAtech, Germany).

4.2.5 Data analysis

All statistical analyses were carried out using the software package Statistica 13 (Stat-Soft Inc., Tulsa, OK, USA). Growth, biomass and physiological parameters were analyzed by three-way analysis of variance (ANOVA) to test for significant main effects of the factors CO_2 concentration, grass competition levels, and watering regimes as well as all factor interactions, followed by Tukey’s HSD post hoc test of pairwise significant differences. Prior to the 3-way ANOVA, all data were analyzed for homoscedasticity using Levene’s test, and data were transformed appropriately where necessary. In addition, residual plots and normal probability plots were inspected to ensure that the assumptions of ANOVA were met.

4.3 Results

4.3.1 Growth conditions

The carbon dioxide concentrations within the chambers were set at constant values of 400 ppm for the ambient chamber and 950 ppm for the elevated chambers. The set values were reached during the daytime, while night-time concentrations were slightly higher due to plant respiration. Deviation from set values was approximately 50 ppm on average. There was a slight, but non-significant difference of relative humidity between the two chambers of ambient and elevated CO_2 averaging at 80 ± 7% and 72 ± 7 % respectively. The temperature in both chambers was 25 ± 2°C for the entire experimental period. Light regimes-sun light, shading and artificial light were measured and resulted in identical irradiation conditions in the two chambers. Overall, the environmental conditions in the two chambers were stable and similar throughout the duration of the study except the ambient CO_2 (400 ppm) and the elevated CO_2 (950ppm).

4.3.2 Effects of CO_2, competition and water availability on shea seedling gas exchange

Elevated CO_2 resulted in a 10% ($p<0.001$) increase in maximum light-saturated apparent assimilation rate (*A*max) and a 14% ($p=0.001$) reduction in stomatal conductance (g_s) as well as an 11% ($p=0.006$) decrease in transpiration rate (*E*) (Table 4.1, Fig. 4.2). Therefore the intrinsic water use efficiency (WUEi) was 22% ($p<0.001$) higher at elevated CO_2. Grass competition significantly reduced maximum light-saturated photosynthesis (*A*max) by 9% ($p<0.001$), while the C/N ratio were increased by 3% ($p<0.001$) (Table1). Watering regimes did not affect any gas exchange parameter but interacted with grass competition and elevated CO_2.

Table 4.1 F-values of three-way ANOVA of all measured physiological parameters of shea seedlings grown under elevated and ambient CO_2, two competition treatments and two watering regimes. n=5

	Sources of Variation						
Parameter	Carbon dioxide (CO_2)	Water (W)	Competition (T)	C*W	C*T	W*T	C*W*T
A_{max} (µmol m^{-2}s^{-1})	**13,84*** **	1,34	**11,13** **	0,22	0,85	0,84	0,01
Vcmax (µmol m^{-2}s^{-1})	0,03	0,71	0,24	0,17	0,03	2,30	0,16
J_{max} (µmol m^{-2}s^{-1})	**28,38*** **	2,06	**56,40*** **	0,02	**4,05* **	1,51	**8,66** **
TPU (µmol m^{-2} s^{-1})	**18,56*** **	3,45	**23,21*** **	**8,70** **	1,39	**45,69*** **	0,04
R_d (µmol m^{-2} s^{-1})	**8,24** **	0,001	0,003	**4,69* **	**9,85* **	0,05	0,25
Γ (µmol mol^{-1})	**30,07*** **	3,51	**4,56* **	2,57	**28,01*** **	0,54	1,46
ϕ	2,71	1,50	**53,11*** **	**8,67** **	1,202	**6,94** **	**6,81** **
*I*c (µmol m^{-2} s^{-1})	1,59	2,75	1,30	0,31	0,54	0,12	1,19
g_s (mol m^{-2}s^{-1})	**40,95*** **	0,59	0,17	0,08	**5,59* **	**5,61* **	0,01
E (mmol m^{-2}s^{-1})	**8,44** **	2,97	0,09	0,01	0,24	**15,08** **	3,56
WUE_i (µmol mol^{-1})	**27,84*** **	0,69	0,63	1,56	3,28	0,73	0,69
C/N ratio of leaves	**7,18** **	**6,18* **	**5,25* **	**4,69* **	1,00	3,56	0,73
Specific leaf area (cm^2 g^{-1})	0,28	0,78	3,94	0,04	0,99	1,81	0,79
Leaf area ratio (cm^2 g^{-1})	**13,39*** **	1,60	2,49	3,16	**4,38* **	2,61	2,83
Leaf mass per area (g cm^{-2})	**24,53*** **	0,35	0,26	**6,37* **	2,92	1,12	0,74
Specific root length (cm g^{-1})	0,11	0,37	2,14	2,53	0,31	0,00	2,12
Root to shoot ratio	0,35	**5,79* **	**7,25** **	3,31	0,46	1,96	0,54
Leaf mass fraction (cm^2 g^{-1})	0,61	1,78	**49,50*** **	0,08	0,37	**5,92* **	0,23
Stem mass fraction (g g^{-1})	**16,47*** **	1,70	**35,95*** **	0,15	3,16	3,29	0,94
Root mass fraction (g g^{-1})	0,87	1,10	**45,96*** **	0,02	0,43	**4,36* **	0,16
Above-ground biomass (g)	3,79	3,71	**60,60*** **	2,60	0,46	2,60	0,36
Below-ground biomass (g)	0,21	0,01	**9,97** **	0,89	0,55	0,64	0,52
Total biomass (g)	0,3	0,14	**26,09*** **	0,12	0,52	2,42	0,32

*A*max, maximum light-saturated photosynthesis rate; V_{cmax}, maximum Rubisco carboxylation ratio; J_{max}, maximum electron transport rate; TPU, triose phosphate utilization rate; R_d, dark respiration rate; Γ, CO_2 compensation point; ϕ, apparent quantum yield; Ic, light compensation point; g_s, stomata conductance; *E*, maximum transpiration rate; WUE_i, intrinsic water use efficiency.

Statistically significant values in bold; * <0.05, **<0.01, ***<0.001 probability levels

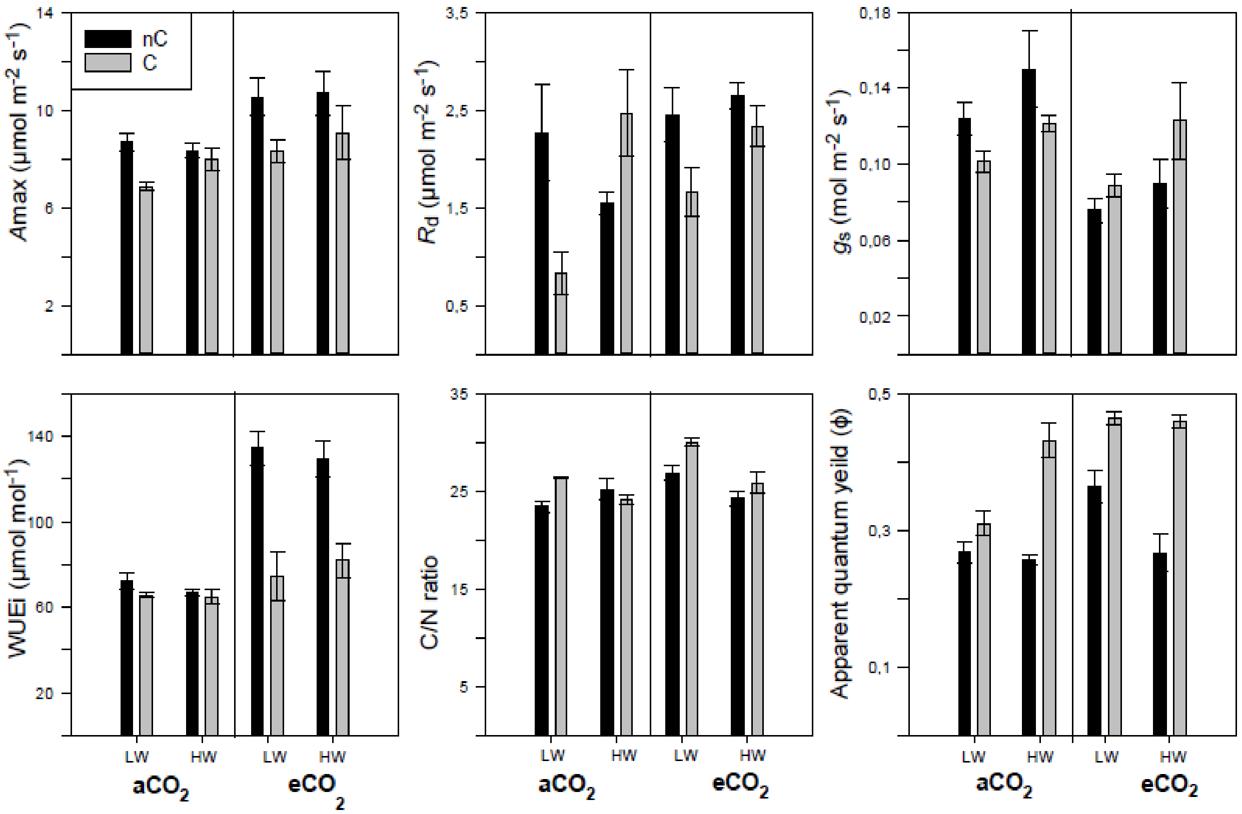

Fig. 4.2 Effects of CO$_2$ concentrations, grass competition and water availability on gas-exchange parameters. Hw=High water, Lw= Low water,C= grass competition, nC= no grass competition. Mean ± SE. n=5

Two-way interactions of CO$_2$ and competition were recorded for stomatal conductance, dark respiration and the CO$_2$ compensation point (Table 4.1). The stomatal conductance was reduced significantly in plants exposed to eCO$_2$ in treatments without grass competition (p=0.022), whereas under competition the stomatal conductance was not significantly affected by eCO$_2$. Dark respiration increased in eCO$_2$ treatments, however there was a significant (p=0.035) difference in only non-competition treatments with high water and in competition treatments with low water. The CO$_2$ compensation point (Γ) was significantly different ($p<0.001$) between non-competitive treatments in aCO$_2$ and eCO$_2$ (Table 4.1).

We also recorded two-way interactive effects between water availability and competition on dark respiration and C/N ratio. The C/N ratio recorded significant (P=0.035) increases in eCO_2 treatments with low watering regime (Fig. 4.2). We also recorded three way interactive effects of CO_2, grass competition and water availability on *J*max and θ both of which are related the light reactions of photosynthesis. Grass competition decreased *J*max significantly (p=0.005) in both low and high water availabilities in both CO_2 concentrations (Table 4.1). Grass competition treatments under both CO_2 concentrations and water levels recorded significantly (p=0.012) higher ϕ values.

4.3.3 Shea seedling growth and biomass response to eCO_2, grass competition and water availability

Elevated CO_2 increased leaf area ratio (LAR) by 21% ($p<0.001$) and the stem mass fraction (SMF) by 13% ($p<0.001$) as in Fig. 4.3 and Table 4.1. The root to shoot ratio (R:S) was 24% (P=0.02) higher in well-watered seedlings however, it was also 21% (P=0.01) higher in treatments with grass competition. Interactive effect of carbon dioxide and watering regimes (P=0.015) with aCO_2 recording higher LMA in all treatments except in no competition, low water seedlings. We observed a two-way interactive effect of carbon dioxide and grass competition on LAR (P =0.041) with higher leaf area in eCO_2 growth, but the effect prominent in non-competition treatments (Fig. 4.3).

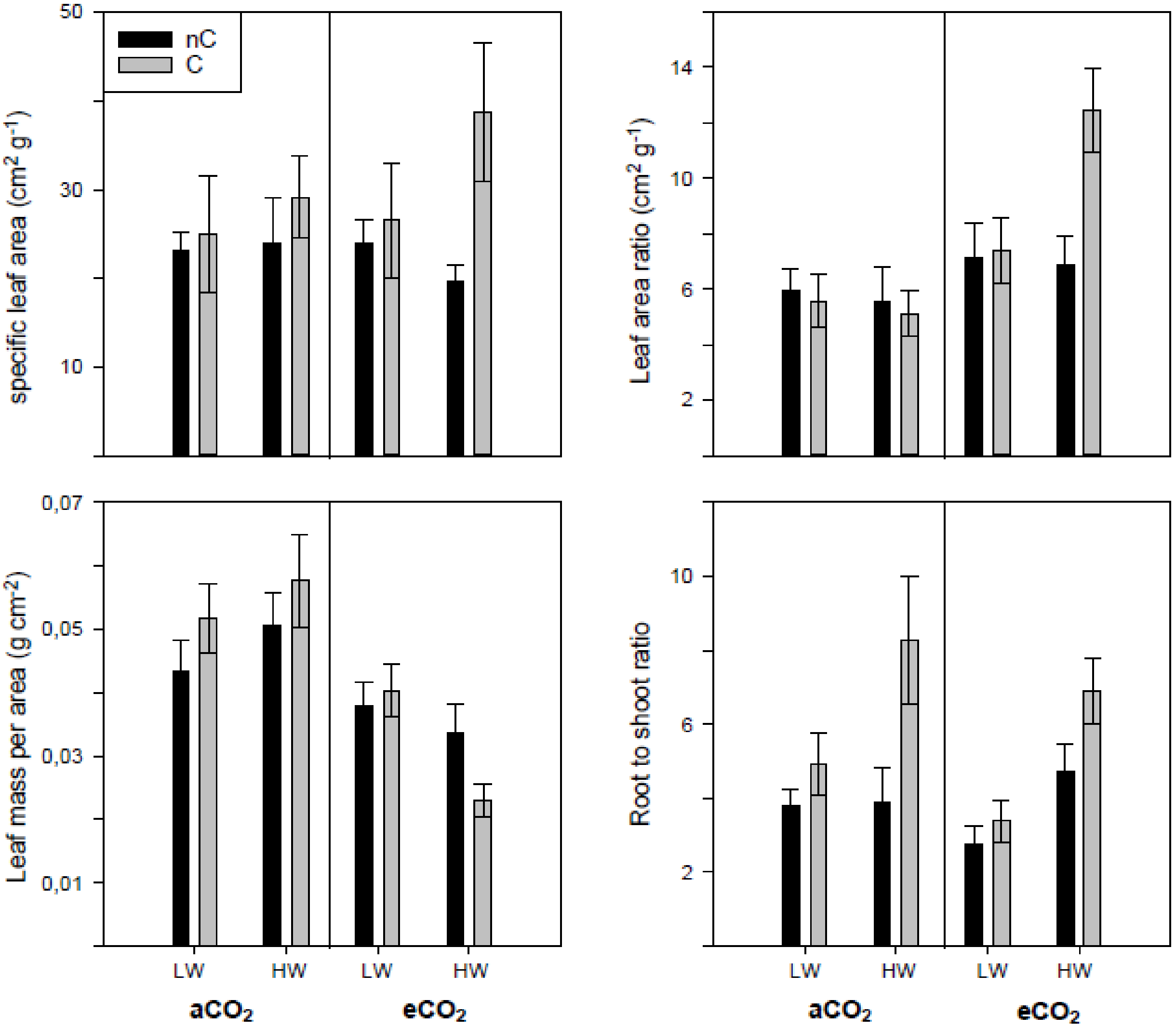

Fig. 4.3 Effects of CO_2 concentration, grass competition and water availability on shea seedling growth. Mean ± SE. n=5

Grass competition significantly reduced by 19% ($p<0.001$) the SMF (Table 4.1) while the biomass parameters; ABG, BGB, TB (Fig. 4.4) were all reduced significantly by 39% ($p<0.001$), 25% ($p=0.003$) and 28% ($p<0.001$).

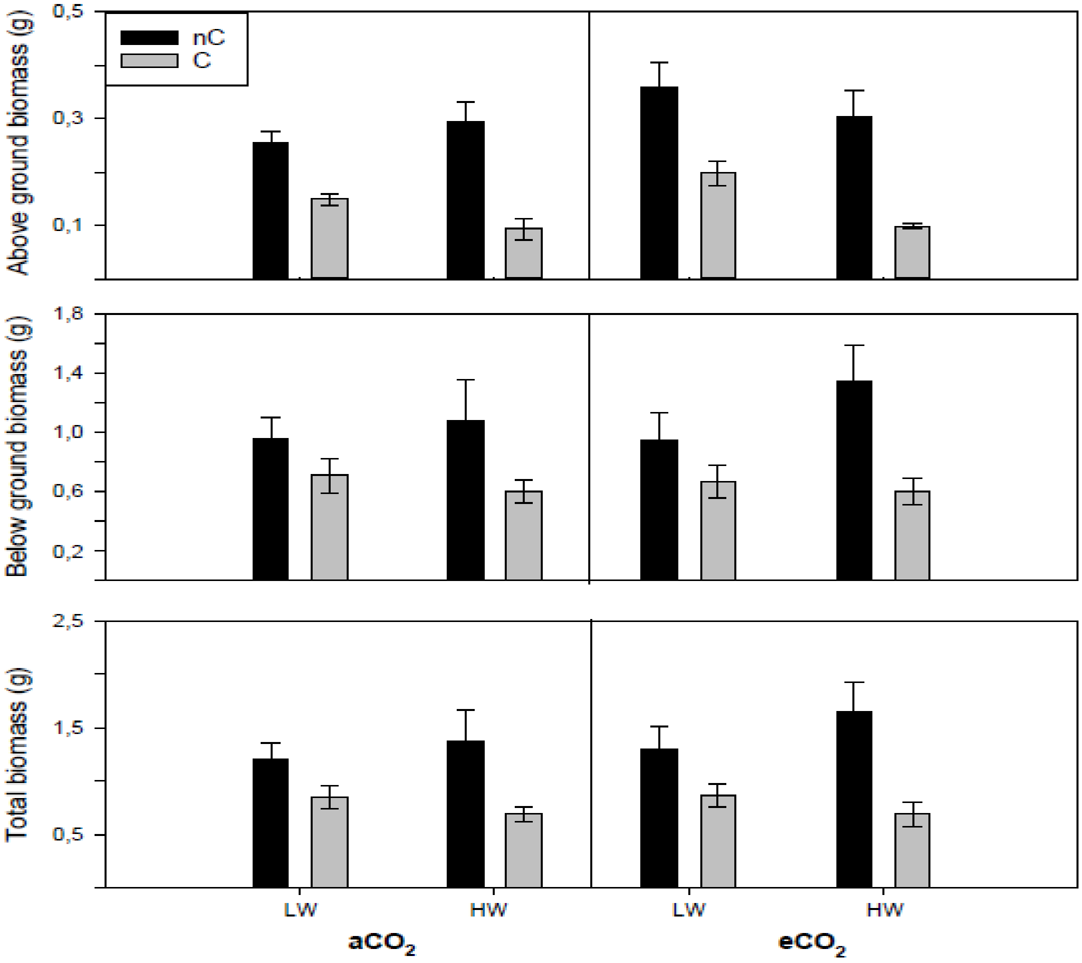

Fig. 4.4 Effects of CO_2 concentration, grass competition and water availability on shea seedling biomass allocation. Mean ± SE. n=5

4.4 Discussion

4.4.1 Gas exchange in shea seedlings

The aim of this experiment was to assess the extent to which the performance of shea seedlings would be affected by future increases in atmospheric concentrations of CO_2, and how the effects of eCO_2 on shea would be modulated by grass competition and water availability. We assumed that elevated atmospheric CO_2 would generally increase shea seedling growth because of higher assimilation rates and under grass competition and, low water availability due to improved water use efficiency (Fig. 4.1). Overall, our expectations were confirmed for the physiological traits of shea. For growth and biomass production however, only competition, but not eCO_2 was the single dominating factor determining shea performance.

Shea seedlings responded by stimulating photosynthesis under eCO_2, a response typical for most C3 plants (Ainsworth and Long 2004; Long et al. 2004; Leakey et al. 2012). Increases in *A*max, *J*max, and triose phosphate utilization (TPU) were recorded under eCO_2. Farquhar et al. (1980) modelled the rate of photosynthesis to be limited by either the concentration of carbon dioxide at the site of carboxylation or the rate of supply of RuBP. Higher *A*max under eCO_2 is partly due to increased concentration of intercellular CO_2 at carboxylation sites thereby competitively mitigating the oxygenation reaction of Rubisco (Drake et al. 1997). In addition, the reported increases in both *J*max and TPU indicate a substantial upregulation of the carboxylation potential, electron-transport and the phosphate-limited parts of the photosynthetic apparatus under eCO_2 in shea seedlings.

The significant increase in C/N ratio may result from a higher N use efficiency (Drake et al. 1997; Leakey et al. 2009) of shea seedlings under eCO_2, together with the shift of control of carbon assimilation from Rubisco towards RuBP regeneration which allows shea to decrease Rubisco content at eCO_2 and enhance their investment in photosynthetic mechanisms. The increase in C/N ratio under eCO_2 could also simply be the result of increased carbohydrates content (Drake et al. 1997). The carbon dioxide compensation point (Γ) defined as the substomatal concentration of CO_2 at which no net assimilation occurs, increases with eCO_2 in this study. Below the Γ, respiration of plants grown under eCO_2 was increased in high water treatments as well as in treatments without competition thereby occurring under favorable conditions. This response of R_d may also be driven by greater substrate availability (Leakey et al. 2009; Williams and Farrar 1990).

The reduction in g_s reported in shea is a general occurrence in most plants under eCO_2 (Ainsworth and Rogers 2007; Long et al. 2004; Leakey et al. 2012; Wand et al. 1999), but the effect is also subject to environmental feedbacks (Herrick et al. 2004; Leakey et al. 2006; Naumburg et al. 2003; Nowak et al. 2004). However, our results show that grass competition did not significantly decrease g_s under eCO_2. Accordingly, the hypothesized gain of competitiveness of the C3 plants against C4 grass under eCO_2 lacks its mechanistic rationale. In this study, decreases in stomatal conductance together with increased *A*max led to higher WUEi which corroborate earlier reports of the effects of eCO_2 on soil water content that might eventually increase woody tree seedling establishment (Kgope et al. 2009; Polley et al. 2002). Reports of high variation in sap flow between dry and wet seasons indicated that shea transpiration is regulated by climatic variables and water availability (Awessou et al. 2017; Bazié et al. 2017). Therefore increases in CO_2 concentration as a result of climate change will result in a higher water use efficiency of shea seedlings which might help to better withstand water shortage. shea trees are however, capable of hydraulic redistribution with seedlings benefitting from older cognates (Bayala et al. 2008a).

Biotic interactions such as competition to shea seedlings by grass or food crops are typical in parklands. Grass competition negatively affected shea seedling photosynthesis as *A*max, *J*max, TPU and dark respiration (R_d) were all reduced with grass competition. Given the fact that the grasses were fully grown after 90 days, we assume the grasses out-competed the shea seedlings for resources which possibly resulted in low soil water. Davis et al. (1999) suggested woody tree seedlings photosynthesis and growth being highly correlated with water availability. Our results agree with this hypothesis as we recorded interactive (water and grass competition) effects on photosynthetic parameters (*J*max, TPU, Γ and *g*s). Campbell and Holdo (2017) also reported C4 grasses out-competing African savanna tree seedlings resulting in drastic reductions in tree carbon assimilation rates as reported here. Iacono and Sommer (2000) reported the maximum electron transport rate declining with low hydration in Vine grapes which they associated to biochemical /stomatal limitation playing a more vital part in shaping water-stress related decline in photosynthesis than biochemical processes of energy transfer and electron transport. We similarly recorded a declined in *J*max with grass competition across all CO_2 treatments. The grass competition may also have induced shade on shea seedlings which reduced the light intensity received by shea thereby affecting the light acclimation of photosynthesis. The increase in apparent quantum yield in grass competition treatment is an indication of shea being adaptable to low light intensity. Considering the fact that *J*max, ϕ, and the g_s are differently affected by CO_2 concentration under low light (grass competition), we conclude that shea is adapted to low light conditions (shade) as created by tall grass or even older shea trees. Interactive effects of CO_2 on sun/shade leaves have been reported on *Quercus rubra* where growth response was significantly increased in shade under eCO_2 (Cavender-Bares et al. 2000). We therefore agree with the hypothesis that light conditions (shade/light) have important effects on the relative impact of eCO_2 on carbon gain (Urban et al. 2014).

The increases in photosynthesis seem little; however, given the fact that shea is not a fast growing tree species, these could have marked ecosystem effects by promoting seedling establishment and sapling escape from the flame zone. Increased recruitment of adult shea trees can change agroforestry parklands with implications for carbon sequestration, ecosystem services as well as economic implication for landowners. On the other hand the decreases of assimilation rates caused by grass competition should be a worry as grass control is paramount to shea seedling establishment. *Cenchrus pedicellatus* grown under eCO_2 was, however, reported to also have a tremendous reduction in stomatal conductance, but no significant change in biomass and C/N ratio (Tom-Dery et al. 2018).

4.4.2 Growth and biomass allocation

Although eCO_2 resulted in increases in photosynthesis, this only occasioned an increase in leaf area ratio and stem mass fraction, but did not significantly increase biomass. The increases in R_d under eCO_2 which involves loss of assimilated carbon might be one reason for the non-significant change in biomass accumulation. We also think shea under eCO_2 resorts to allocation of surplus assimilates to the stem as is evident in the significant increases in stem mass fraction. Nevertheless, Bayala et al. (2017) reported the leaf area rather than the seedling height as the most important growth parameter of shea seedling growth.

Grass competition however, reduced LMF and LAR which is consistent with findings of Pillay and Ward (2014) who reported a positive relationship between SLA and tree competitive response across four savanna tree species. February et al. (2013) similarly reported increasing rainfall acting to increase the competitive pressure exerted by grasses on trees which negatively affected tree growth. Campbell and Holdo (2017) have described competition between African savanna C4 grasses and tree seedlings as asymmetric in favor of grasses resulting in reductions in tree seedling growth rates. In this study, all biomass parameters (AGB, BGB and TB) were significantly reduced by grass competition as was reported previously (Bond 2008; Kiaer et al. 2013) and mainly attributed to root competition. However, Manea and Leishman (2015) reported similar suppressive effects from both grass root and stem competition on total biomass of tree seedlings.

It has previously been reported that grasses compete with shea for space, light and nutrients as well as act as a source of combustible material that intensifies periodic bushfires (Osei-Amaning 1996). The implications of grass competition to shea seedlings are severe, especially since shea is not a fast growing tree. For shea seedlings to be able to cross over to the sapling stage and escape the fire trap or bottlenecks, grass control seem to be necessary. In agroforestry systems, shea seedlings take advantage of cultural practices by farmers like weeding to control grasses for their crops to grow to the sapling stage.

4.5 Conclusion

Photosynthetic carbon uptake in shea seedlings was enhanced by eCO_2. The increases in photosynthesis as a result of eCO_2 though, did not result in significant increases in biomass but rather increased allocation to stems. However, also leaf area ratio and stem allocation increased under eCO_2. Furthermore, the stomatal conductance in shea was reduced with eCO_2 and resulted in increased water use efficiency. Future increases in atmospheric carbon dioxide concentration seem therefore to be beneficial to shea seedling growth, especially in areas susceptible to low water availability. On the contrary, increased grass competition did not only result in a reduction of photosynthetic and dark respiration rates, it also resulted in decreases in growth, reduced allocations to leaves and stems and all biomass parameters. Control of grass competition is therefore recommended for securing initial shea growth.

4.6 Acknowledgements

We wish to thank all the greenhouse staff, especially Willi Göslin, Marion Klötzl, Maren Winnacker for their help in the greenhouse. We also acknowledge the contributions and suggestions of Jasmin Vuralhan-Eckert and Detlef Böhm. We also thank GETFUND for sponsoring the first author.

CHAPTER FIVE

5 EXCELLENT SHEA (*VITTELARIA PARADOXA* C.F. GAERTN.) SEEDLINGS RECOVERY AFTER FIRE: GAS-EXCHANGE, GROWTH AND BIOMASS PARTITIONING ASSESSMENT

Damian Tom-Dery[1,2], Kai Jensen[1]and Christoph Reisdorff[1]

Manuscript submitted (Forest, Trees and Livelihoods)

5.1 ABSTRACT

Fire can be seen as a generalist herbivore of vegetation and is presumed to be intensified by climate change in savannas. Shea (*Vitellaria paradoxa* C.F. Gaertn) is native to the savanna ecosystem, an ecosystem prone to periodic bushfires due to the long dry season and accumulated combustible biomass. We studied the effects of simulated fire on shea seedlings gas exchange, growth and biomass allocation in a greenhouse experiment. We hypothesized that fire decreases photosynthetic performance of regrown leaves leading to lower growth and altered biomass allocation in shea seedlings. Sixteen weeks after fire treatment, the maximum light saturated photosynthesis, apparent quantum yield, the maximum electron transport rate and water use efficiency at the leaf were higher in the control treatment but not significantly different from fire treatments. However, the fire treatments recorded higher but not significant differences of gas exchange parameters: maximum carboxylation potential, dark respiration, light compensation point and the stomatal conductance. Fire treatments showed non-significantly higher specific leaf area, aboveground and total biomass; whereas all other measured growth parameters and belowground biomass were higher in the control treatments. Shea seedlings have therefore shown exceptional recovery to gas exchange performance, growth and biomass allocation patterns four months after fire.

Keywords**:** Biomass, Fire, Gas-exchange, Photosynthesis, Growth, Recovery, Savanna, Shea

5.2 INTRODUCTION

Agroforestry parklands are considered the most widespread farming system in the Sahelian zone (Bayala et al. 2015) of which shea (*Vitellaria paradoxa* C. F. Gaertn.) is a major component. Shea distribution extends from Senegal to the foothills of the Ethiopian highlands (White 1983) across 21 countries (Boffa 2015; Naughton et al. 2015). Throughout this area, an estimated actual number of productive trees and the estimated potential number of productive trees scales from several hundred millions (Lovett 2004) to a few billions (Naughton et al. 2014). Shea trees therefore make-up a high-percentage of standing biomass thus protecting the environment against soil degradation and holding noteworthy carbon stores with high potential for future C-sequestration aimed at climate change mitigation (Luedeling and Neufeldt 2012).

The savanna environment exposes shea to two characteristic hazards: drought stress (4-8 months without rain) (Vermilye 2004; Nikiema and Umali 2007) and the yearly bushfires that usually occur in the dry season (Furley et al. 2008). After successful germination of the seed, shea seedlings are confronted by the dry season with its attendant drought stress and fire hazards, both of which lead to defoliation (Nikiema and Umali, 2007). Fire can be regarded as a key generalist herbivore of biomass (Bond and van Wilgen 1996) and consumes any combustible material in its path (Bond et al. 2005). Higher fuel load influences the intensity of bushfires (Wade 2011) with the grass vegetation providing the fuel for burning in savanna ecosystems (Ramos-Neto and Pivello 2000). Across the savanna, the combustible fuel load is low during late burning resulting in flame temperature between 235 - 496°C (Kugbe 2012).

The harshness of the savanna ecosystem notwithstanding, shea is known to grow well in this environment and even dominate these landscapes. Apart from human intervention by way of anthropic selection (Lovett and Haq 2000), shea has developed adaptive features such as the cryptogeal germination process which involves the burial of the plumule below ground (Jackson, 1968) and the development of a strong and solid root system early in the life-cycle of the seedling (Jackson 1968; Adomako 1985; Ugese et al. 2010). Adult trees also have suberized bark which offers resistance to annual bushfires (Hall et al. 1996; Nikiema and Umali 2007). There is little information on the eco-physiological reaction patterns of shea (Bayala et al. 2008; Tom-Dery et al. 2017) except for sap flow (Awessou et al. 2017; Bayala et al. 2009; Bayala et al. 2008; Bazié et al. 2012), water regimes and seedling traits (Glèlè Kakaï et al. 2011; Bayala et al. 2017) and the effects of elevated CO_2 on shea seedling growth (Tom-Dery et al. 2018). Shea is reported to have remarkable attributes of recovery after disturbance (Hall et al. 1996; Nikiema and Umali 2007), however, without empirical proofs apart from defoliation studies (Ugese et al. 2011; Ugese et al. 2015). To our knowledge, there are no studies on the gas exchange and biomass partitioning processes after fire which causes total defoliation of shea seedlings. These processes are crucial to understanding the mechanisms that facilitate shea adaptation and productivity in the savanna environment. The objectives of this study were to (1) assess shea seedlings gas exchange after regrowth following simulated fire and (2) to evaluate the effect of simulated fire on shea seedlings growth and biomass allocation. We hypothesize volatilize organic N of aboveground biomass due to fire leads to severe N loss per plant and in top soil, and this will result in lower photosynthetic rates in fire treated seedlings because, N sufficiency is a prerequisite to a well functional photosynthetic system. However, if the photosynthetic parameters are not evidently affected and the plants' growth rate/biomass accumulation is not noticeably lesser than the control, this might indicate good resilience of shea seedlings to burning.

5.3 MATERIALS AND METHODS

5.3.1 Plant preparation and growth conditions

Seeds for the study were picked from 20 trees located in Tolon (09° 25'N and 00° 58'W) in the Guinea savanna zone of Ghana. Seeds were transported within one week of picking to the greenhouse of the University of Hamburg (53° 30'N and 10° 12'E) where they were germinated in germination trays. The pre-germination lasted a period of 6 days and was followed by transfer into 7L plastic pots of height 21cm filled with a mixture of 2:1 (w/w) fine sand (10-20mm) and standard substrate (TKS1, Floragard Vertriebs-Gmbh, Oldenburg). The bottom of the pots was tightened with a plastic mesh to prevent loss of substrate during watering. It took a total of 8 weeks to complete the germination process. After pre-treatment growth, the pots were randomly placed in a greenhouse with controlled growth conditions (Day/night air temperature 30°C/22°C; 40-84% relative air humidity; Length of photoperiod same as Hamburg area) and allowed to grow for two years.

Two year old shea seedlings were subjected to simulated late burning which usually occur in first quarter of the year with reported mean flame temperatures of 235°C - 496°C (Kugbe 2012). Based on the reported fuel load of 2-3 t ha^{-1} in the Ghanaian savanna (Saarnak 1999), we extrapolated to 76g m^{-2} per pot area of 0,038m^{2} supposing 2 t ha^{-1} fuel loads. Dried grasses of *Cenchrus pedicellatus* were weighed (76g) and placed in the pots with one shea seedlings randomly selected for the fire experiment. Prior to placing the grass into the pots, aluminum foil was wrapped around the plastic pots to prevent the pots from burning (Figure 1). Naked fire was torched on the dry grass using bunsun burner flame (Labogaz 206, Campinggaz, Bristol, UK) which was completely burned down. The heat generated by the burning grass was measured using infra-red thermometer (Voltcraft IR-1000-30D, Conrad Electronics SE, Hirschau, Germany). Five pots of shea seedlings were subjected to this simulated burning treatment. Several hours after the fire treatments all pots for the fire treatment and control were watered. Regrowth of the fire treatment started two weeks after fire treatment and took five weeks for 100% regrowth of all shea seedlings.

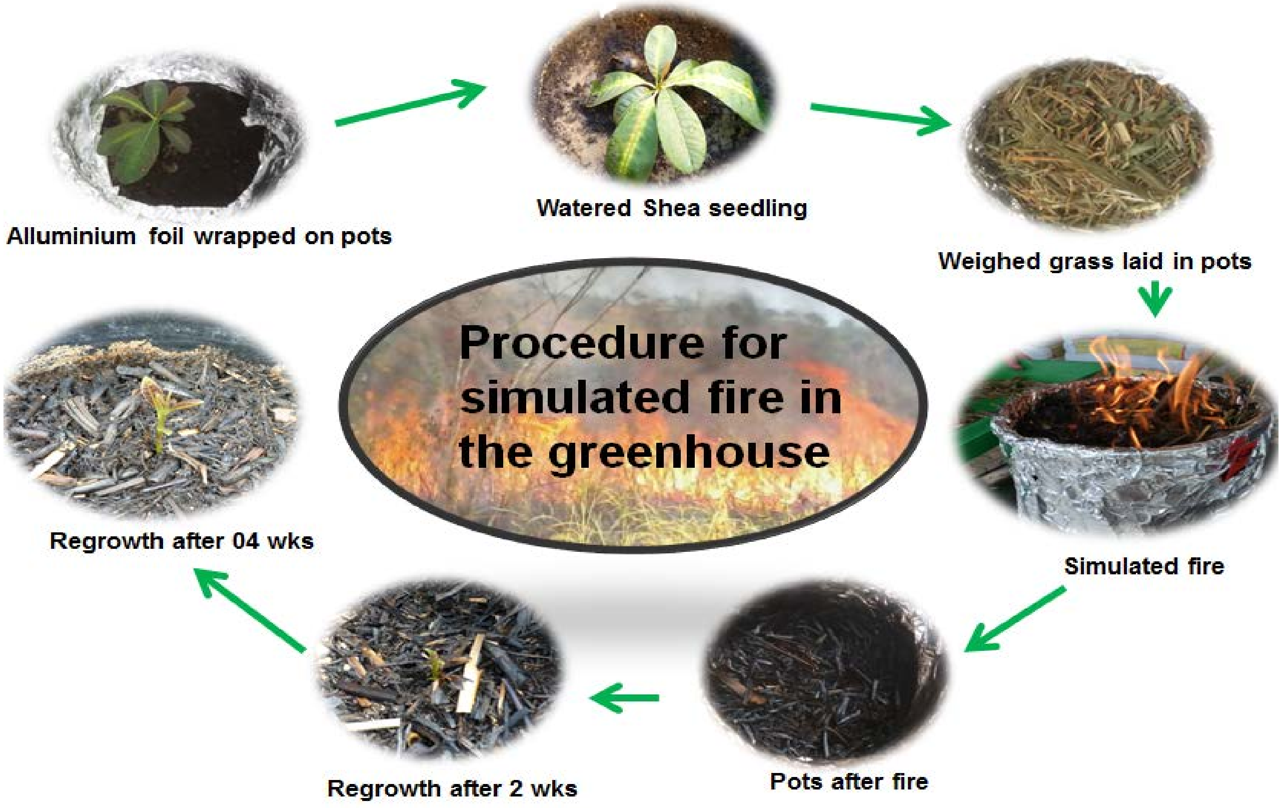

Figure 1 Procedure for stimulated burning in a greenhouse

The complete design of the study comprised a fire treatment and control with five replications each. The pots were randomly distributed on a bench in the climate chamber. To avoid edge and chamber effects, the positions of individual potted plants were rotated on the tables on a weekly basis. The light condition, temperature and air humidity of the chamber was monitored throughout the experiment. The Shea seedlings were left to regrowth and continue growing with normal watering for 16 weeks during the growth period (May-September, 2017).

5.3.2 Gas exchange and physiological measurements

After 16 weeks of growth, the light response curves were measured using the LI-6400XT infrared gas analyzer (LI-COR Biosciences, Inc., Lincln, NE, USA). The light response curves were auto-logged (at a CO_2 concentration of 400 ppm) with a maximum equilibration time of 200 s and a minimum of 120 s. Photosynthetic rates were measured in a descending order at a PPFD of 1800, 1500, 1200, 800, 500, 250, 100, 80, 50, 20, 0 $\mu mol m^{-2} s^{-1}$. The stomatal conductance (g_s) was simultaneously measured with the light response curves and the intrinsic water use efficiency (WUE_i) was calculated by dividing A_{max} by g_s. The maximum light-saturated rate of photosynthesis (A_{max}), apparent quantum yield (ϕ), dark respiration (R_d), and the light compensation point (I_c) were estimated by curve fitting following the model of Buckley and Diaz-Espejo (2015).

To reveal underlying processes responsible for differences in shea performance, we measured CO_2-response of apparent assimilation of shea seedlings by means of A/ci curves (net CO_2 assimilation rate, An, against substomatal CO_2 concentration, Ci). The A/ci curves was auto-logged with a minimum waiting time of 80 s and maximum of 180 s. Assimilation rates were measured in the range of 50-1500 ppm CO_2, starting with 400 ppm and decreasing CO_2 concentrations till the least and thereafter continuing from 400 ppm again increasing to the highest CO_2 concentration. This pattern was used to prevent the deactivation of enzymes at low CO_2 and avoid the induction of stomata closure at high CO_2. The CO_2 compensation (Γ) point was estimated by linear regression from the linear part of the curve below 200 ppm Ci. The maximum electron transport rates (*J*max) predicted by RuBP regeneration limited assimilation rate (Aj) and the maximum carboxylation rates of Rubisco (Vcmax) estimated by Rubisco carboxylation-limited assimilation rate (Ac) were estimated from the A/ci curves using curve fitting utility 2.0 (Sharkey et al. 2007; Sharkey 2016) based on the photosynthetic model of Farquhar et al. (1980) and Dubois et al. (2007).

5.3.4 Plant growth and biomass parameters

Growth characteristics were recorded before harvesting the plants. After harvesting, plants were separated into leaves, stems and roots. Leaves were digitized with a camera (Panasonic DMC-FZ38) and the leaf area was determined with the pixel counting software Image J (Abramoff et al. 2004). The roots were thoroughly washed from the soil mass through a sieve with 1mm mesh size. Roots were scanned with a desk-top scanner (Epson expression 1680) and total root length was determined with Image J (Abramoff et al. 2004). The root thus collected were oven dried (65°C; 48 hours) and weighed as below ground biomass (BGB). Above ground biomass (AGB) was estimated by adding dried weights of leaves and stems, while total biomass (TB) was the total of AGB and BGB.

The measurements were used to estimate seedling traits: leaf mass fraction (LMF; total leaf mass divided by TB, g g^{-1}) , specific leaf area (SLA, leaf area per leaf mass, cm^2 g^-

^{1}), leaf area ratio (LAR, total leaf area divided by TB, cm^{2} g^{-1}), Leaf mass per area (LMA, total leaf mass divided by leaf area), stem mass fraction (SMF, stem mass divided by TB, g g^{-1}), specific stem length (SSL, stem length divided by stem mass cm g^{-1}), and root mass fraction (RMF, root mass divided by TB, g g^{-1}). Leaf traits (LMA, LAR and SLA) were calculated because of their importance to light capture (Poorter 1999), while allocation traits (LMF, SMF, RMF, AGB, BGB and TB) were estimated to illustrate the biomass allocation patterns.

5.3.5 Data analysis

All statistical analyses were carried out using the software package Statistica 13 (Stat-Soft Inc., Tulsa, OK, USA). Growth, biomass and physiological parameters were analyzed by student t-test for significant differences between fire and control treatments. Results are presented as box-plots.

5.4 RESULTS

5.4.1 Burning and chamber climatic conditions

The burning of the grass biomass in the fire treatment lasted on the average 5min ± 0.63min, generating an average heat of 462 °C ± 9°C. Regrowth of shea seedlings of the fire treatment started 2 weeks after burning with two pots of shea seedlings and a 100% regrowth of all pots of plants involved in the fire treatment was achieved after five weeks. Shea seedlings grew well in the chambers and showed no visible signs of nutrient deficiencies or pest attacks (Figure 2).

Figure 2 Image of shea seedling treated to fire (back row) and shea not burnt 16 weeks after burning

5.4.3 Effects of fire on physiological and gas-exchange parameters of shea seedlings

The plants of the control treatment showed non-significantly higher values in maximum light saturated photosynthesis (A_{sat}), (WUEi), the maximum electron transport rate (J_{max}), the apparent quantum yield (ϕ) and the internal water use efficiency (Figure 3).

The plants of the fire treatment, however, achieved higher mean values in the maximum carboxylation potential (V_{cmax}), stomatal conductance (g_s), the carbon dioxide compensation point (Γ), dark respiration (R_d) and the light compensation point (I_c). However, these increases were not significant.

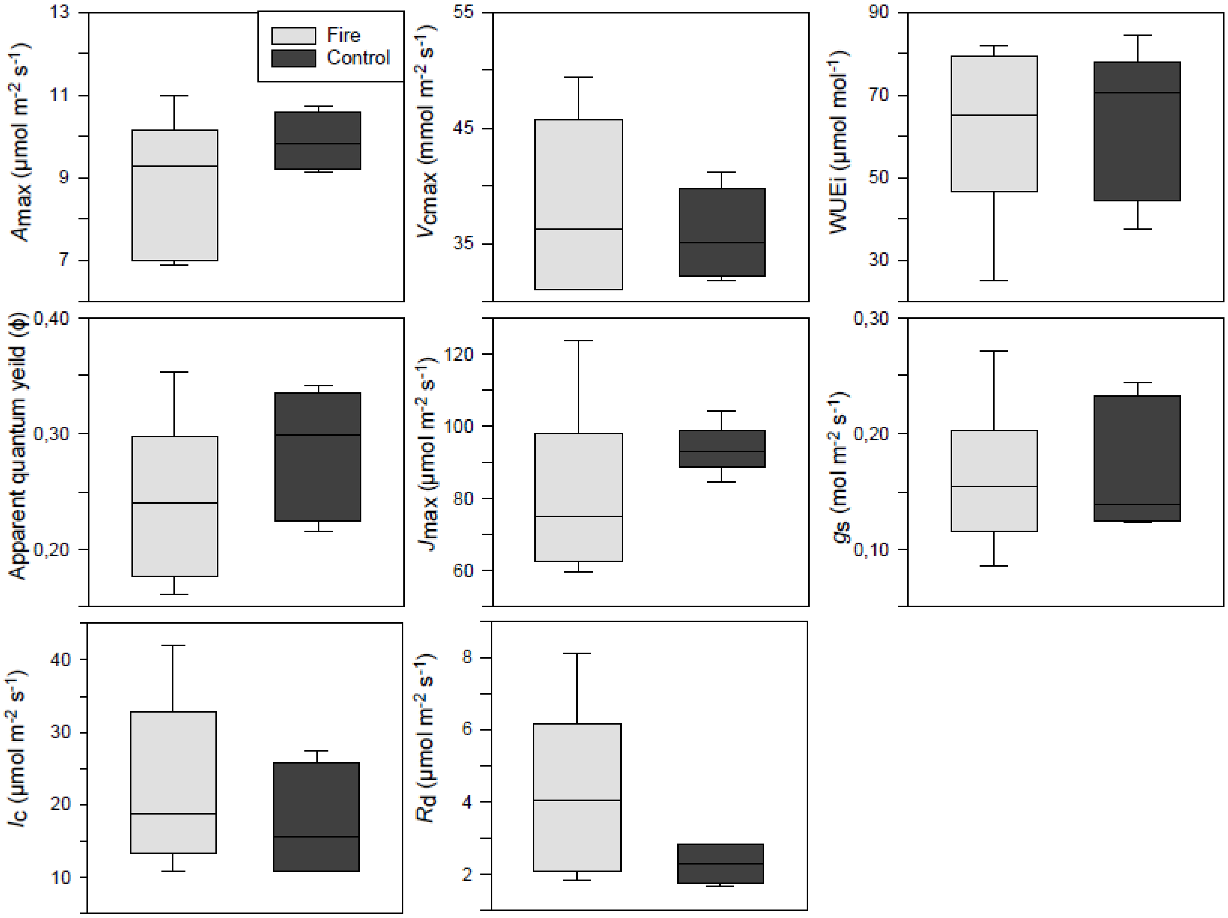

Figure 3 Gas-exchange parameters of shea plants from fire treatment and the control. Student t-test at P=0.05 recorded no significant difference of all parameters. n=5

5.4.4 Growth and biomass parameters response to fire

The growth parameters of all shea seedlings were not significantly different according to student t-test. The plants from control treatments were superior to the burnt treatments in leaf mass per area (LMA) and leaf area ratio (LAR) while, the regrowth of shea seedlings showed higher specific leaf area (SLA) (Figure 4).

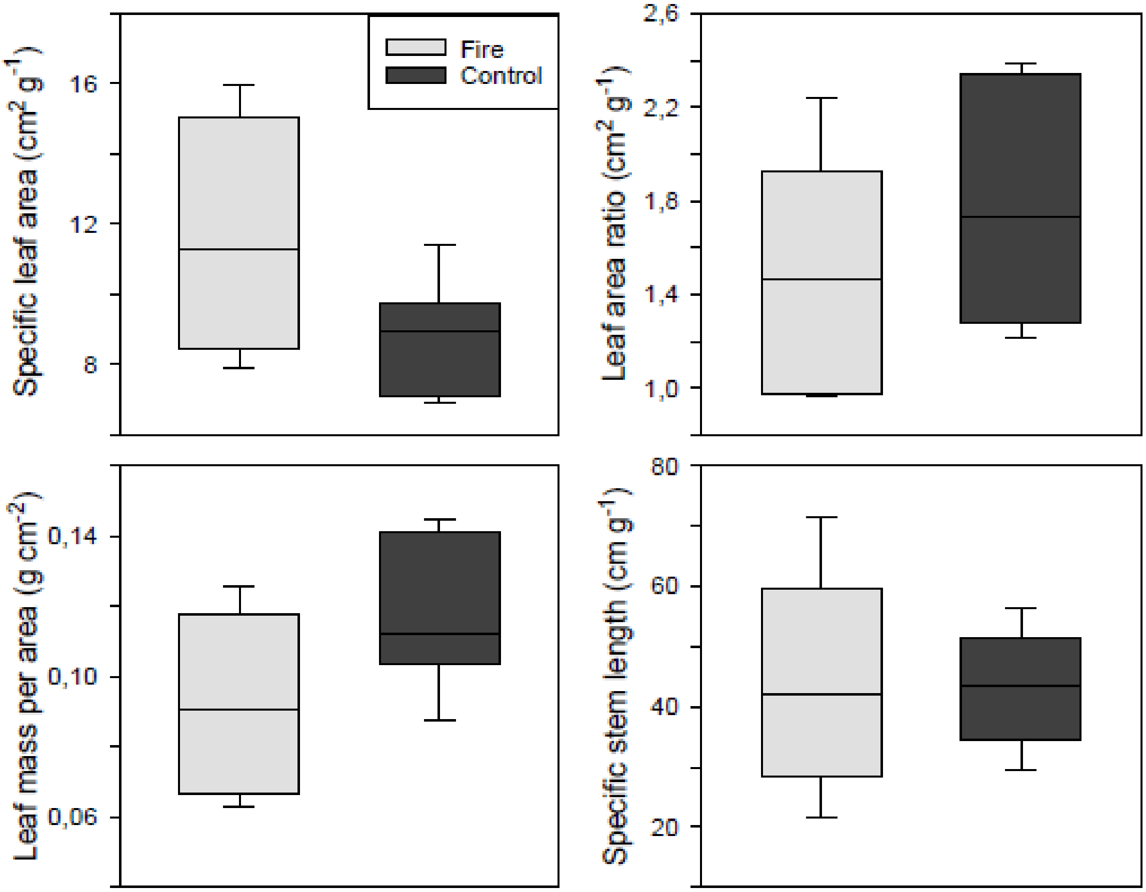

Figure 4 Growth parameters of shea plants from fire treatment and the control. Student t-test at P=0.05 recorded no significant difference of all parameters. n=5

Biomass allocation patterns did not significantly differ between the two treatments. The leaf mass fraction (LMF), stem mass fraction (SMF), root mass fraction (RMF) and belowground biomass (BGB) were higher in control treatments; while the aboveground biomass (AGB) and total biomass (TB) were higher in post-fire regrowths (Figure 5).

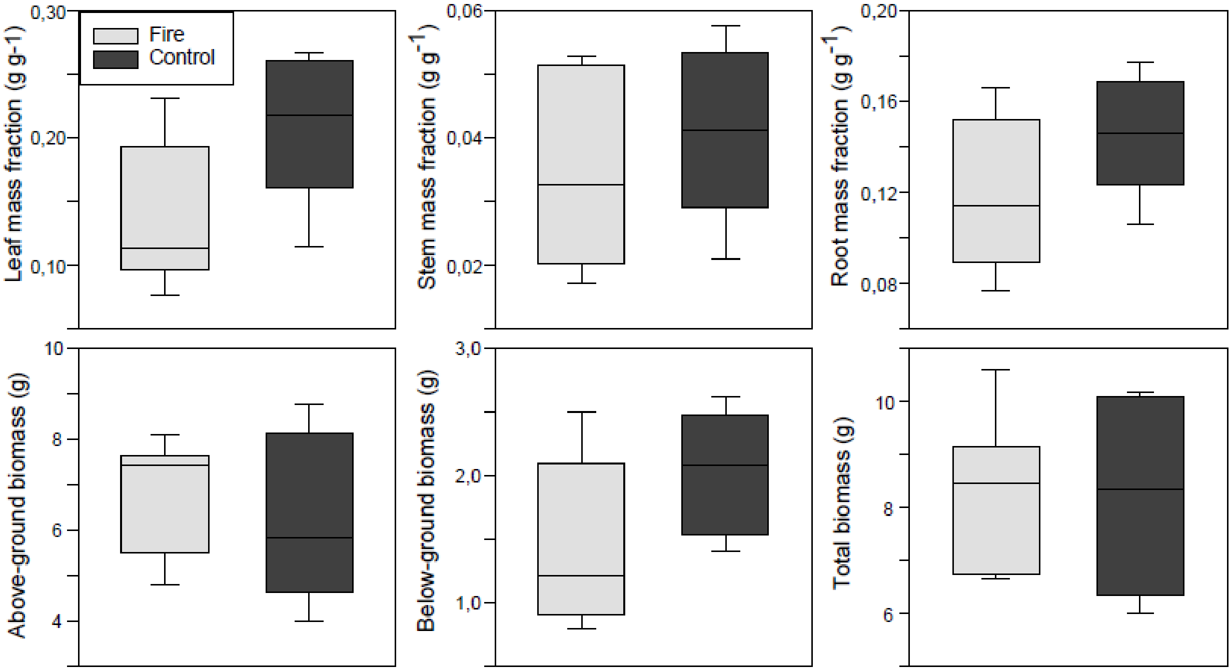

Figure 5 Biomass allocation parameters of shea plants from fire treatment and the control. Student t-test at P=0.05 recorded no significant difference of all parameters. n=5

5.5 DISCUSSIONS

5.5.1 Gas exchange in post-fire shea seedlings

The simulated burning experiment in the greenhouse seem to be a better method of mimicking bushfire than the experimental clipping (defoliation) since fire involves other processes (heating the soil, remains of debris) than complete loss of aboveground biomass. The observed 5 minutes time period and heat generated (462°C) by the stimulated burning is in the same range as values recorded in natural bushfires in savanna (Kugbe 2012). The aim of this research was to investigate the effect of fire on shea seedling gas-exchange, growth and biomass allocation.

Thermal stress is known to increase the Ribolose-1,5-bisphosphate carboxylase/oxygenase activity in plant leaves (Fleck et al. 1996; Crafts-Brandner and Law 2000; Luo et al. 2011). However, here newly regrown leaves were used in all measurements. There are also reports of low photosynthetic rates after thermal stress attributed to the inactivity of Rubisco (Luo et al. 2011). N limitation is known to lead to a decrease in Rubisco activity and thus, lower photosynthetic rate (Leakey et al. 2012). However, Fleck et al. (1996) reported higher photosynthetic rates of regrowths after fire. In savanna species *Acacia karroo*, A_{max} of regrowths was initially higher than unburnt plants, but similar rates were recorded afterwards (Schutz et al. 2009). The non-significantly high stomatal conductance reported here was similarly recorded in post-fire regrowths under good growth conditions (lower temperatures in June) however, under unfavorable conditions (higher temperatures in July) there was an increase in stomatal conductance (Fleck et al. 1998). The higher but non-significant increase in dark respiration of fire treatments was similarly recorded in two herbaceous species after prescribed burning in the Appalachian mountains, USA (Huang et al. 2007). The little increase in dark respiration of fire treatments suggests a higher demand of regrowths for energy to build the carbon skeleton to sustain growth. We assume the regrowths are fast growing thereby have higher rates of nitrate reduction in their roots which increases their respiratory quotient (Lambers et al. 2008). This response of dark respiration could also be driven by greater substrate availability (Williams and Farrar 1990; Leakey et al. 2009). The light compensation (I_c) which is the light intensity at which the rate of respiration and photosynthesis are the same likewise increased in fire treatments as characteristic of younger leaves than older leaves or sun leaves versus shade leaves in control treatments (Pallardy 2008). The similar ϕ recorded is because intrinsic quantum yield varies little from the mean values in shade or light adapted leaves of C3 plants (Singsaas et al. 2001; Lambers et al. 2008).

The non-significant changes of all photosynthetic parameters in this study indicate post-fire photosynthetic plasticity of shea seedlings. The physiological plasticity of shea leads to a full recovery of photosynthetic performance after fire; which implies that even the very young seedlings must have stored beforehand enough C, N and energy in its underground parts to reestablish nearly completely without any functional shortcomings.

5.5.2 Growth and biomass responses to fire

Leaf area is reported to be the most important parameter to measure growth in shea (Bayala et al. 2017). Thus, we estimated several leaf traits in this study. Fire treatment showed non-significantly higher values in the specific leaf area which is an indication of higher metabolic activity and plays a role in determining the rate of carbon assimilation (Schulze et al. 2005). In *Acacia karroo*, similar total leaf area was recorded for burnt and unburnt plants 5 months after fire (Schutz et al. 2009). SLA similarly did not vary in Ponderosa pine between control, thinned and fire regrowths (Sala et al. 2005). The leaf area ratio (LAR) was higher in control treatments and is reported to be a product of relative growth and net assimilation rate (Poorter 1999). The leaf mass per area of *Quercus ilex* resprouts after fire were higher than the controls with a correlated higher leaf nitrogen and total soluble protein (Fleck et al. 1996), however, we recorded a non-significant increase in leaf mass per area in control treatments. Higher leaf mass fraction is an indication of lower leaf construction cost and is typical of deciduous species (Franco et al. 2005). There are, however, reports of leaf lifespan being positively correlated to the LMA (Russo and Kitajima 2016). Defoliation studies on shea also reported no significant changes in leaf area of control and defoliated plants (Ugese et al. 2011; Ugese et al. 2015). The non-significant differences in all leaf area trait parameters are an indication of remarkable recovery of shea seedlings four months after fire.

The similar specific stem length (SSL) of shea seedlings subjected to fire and control may be very revealing. As shea is a slow growing plant any increase in height may be important for the plant escaping the next fire and growing into the sapling stage. The lower root mass fraction after fire reported here is a good functional trait for shea as the roots are vital to survival with the substantial replacement of the used root resources. The root system is therefore very important to its survival especially in challenging instances as faced in the savanna during the dry season with its attendant fire. Jackson (1974) has associated the plumule burying cryptogeal germination of shea and other savanna species to their evolution in a habitat that has long been subjected to annual burning and called them pyrophytic species.

All biomass parameters of control treatments were higher but not significantly different from fire treatments as was reported by Gignoux et al. (2016) who compared growth and survival of savanna and forest tree species treated to fire and shading. Lamont et al. (2011) have suggested there are several fitness benefits of post-fire regrowths that center around their rapid return to adult growth rates. Defoliation studies on shea recorded similar dry matter partitioned to the root and above ground biomass of control and totally defoliated seedlings (Ugese et al. 2011). However, Ugese et al. (2011) suggest the possibility of an emergency measure of shea roots transferring resources for shoot replacement after stress (defoliation or fire), with higher efficiency of the newly formed leaves making it needless for the root to continually act as a secondary source of assimilates. Generally, post-fire regrowth's rely on carbohydrate reserves to support growth and respiration until the plant has recovered enough leaf area to once again actively sustain these costs (Chapin et al. 1990; Iwasa and Kubo 1997). There are reports that root starch that was depleted during post-fire regrowth is subsequently replenished once the plant has recovered enough photosynthetic biomass in savanna woody plants (Miyanishi and Kellman 1986; Schutz et al. 2009). The fact that shea prioritize the root development first after germination before shoot development (Adomako 1985), is indicative it will also allocate more resources to the roots in anticipation of stressful situations like defoliation/fire. Alfaro-Sánchez et al. (2016) suggest post-fire growth responses of Aleppo pine to be dependent on the site water availability and fire severity. However, we suggest that there was sufficient N in the belowground parts of shea seedlings subjected to fire for the rapid regrowth of shea after fire. The overall non-significant difference between fire treated and control shea seedlings in both growth and biomass allocation parameters is an indication of exceptional recovery four months after fire.

5.6 CONCLUSION

In conclusion we propose the above simulated burning experiment as a good way of mimicking bushfire/savanna fires. The similar rates of gas-exchange, growth and biomass parameters four months after fire suggest that shea is well adapted to the environmental stresses posed by the extensive dry seasons which climaxes in imminently increasing risk of fires of the savanna.

5.7 ACKNOWLEDGEMENTS

We wish to express our profound gratitude to our greenhouse staff, Marion Klötzl and Maren Winnacker for their help in the greenhouse. We also acknowledge all the contributions and suggestions of Detlef Böhm.

BOX ONE

B.5 Allocation patterns of carbon and nitrogen in shea (*Vitellaria paradoxa* C.F.Gaertn.) after stimulated late burning

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Manuscript under review for Trees

B.5.1 Abstract

Key message **N balance and reallocation patterns to organs aid to maximize plant vitality after fire in shea.**

Savanna tree species like shea vary in the magnitude of their response to fire, but the functional traits that explain this disparity remain largely unknown. To address this gap, we simulated late burning on shea’s vigor and investigated the allocation patterns of carbon and nitrogen in seedlings, measuring leaf pigments, chlorophyll fluorescence, carbon and nitrogen content of organs (leaves and roots) and C stable isotope ratios in unburnt seedlings and in seedlings regrown after burning in a controlled greenhouse experiment. We hypothesize that after fire treatment N is depleted in all organs since it is allocated from roots to stems and to newly formed leaves. We found a low N-content in all organs (leaves and roots) of fire treatments which were manifested in low chlorophyll/N and Fv/Fm ratio indicating good recovery of shea. Though the $\delta^{13}C$ was not affected by the treatments, we recorded different $\delta^{13}C$ isotopes in shea leaves and roots. We conclude that N balance and reallocation patterns to organs aid to maximize plant vitality after fire in shea.

Keywords: Carbon, Nitrogen, recovery, regrowth, shea

B.5.2 Introduction

Fire is a global biogeochemical agent (Bowman et al. 2009), influencing vegetation structure (Bond & Keeley, 2005) and carbon cycling (Ryan 2009). Fire can act as a top-down control of ecosystem structure because it has similar effects of a generalist herbivore of vegetation (Bond and van Wilgen 1996; Bond 2008). There is a direct relation between fuel load and the intensity of bushfires (Engber et al., 2011) with the grass vegetation providing the required fuel in savanna ecosystem (Oliveras & Malhi, 2016). The combustible fuel load across the savanna is higher for early burns than in late burns because of substantial consumption of fuel load during early burns resulting in higher flame temperature between 492 - 675°C compared to 235 - 496°C for late burns (Kugbe, 2012).

Shea is native to the savanna belt of Africa (White 1983) where fire influences species distribution and ecosystem structure (Bond, 2008). Although shea seedlings are credited with impressive recovery capacities after disturbance (Hall et al., 1996), supporting empirical studies are scarce except defoliation studies (Ugese et al., 2015; Ugese et al., 2011). We studied the effects of simulated late burning on the plant's vigor by investigating the allocation patterns of carbon and nitrogen in shea seedlings measuring leaf pigments, carbon and nitrogen content of organs (leaves and roots) and C stable isotope ratios in unburnt (control) seedlings and seedlings regrown after burning. We hypothesize that after fire treatment nitrogen (N) is depleted in all organs since it is allocated from roots to stems and to newly formed leaves, however, failing to completely meet the leaves' demand. As consequence, N could become a bottleneck for the development of a well-balanced photosynthetic apparatus: If N limits the synthesis of enzymes for the Calvin cycle; this may lead to an imbalance between photosynthetic electron transport and light-independent reactions. Such imbalances can promote photo damage in the photosystem II complex due to over energization, detectable via the fluorescence parameters maximum quantum yield of photosystem II (Fv/Fm) or the performance index (PI). A lower carboxylation potential might also be detectable as a higher discrimination of $^{13}CO_2$ due to higher pi CO_2. However, if the degree of such imbalances does not evidently affect the plants' vigor, this might indicate good resilience to burning.

B.5.3 Materials and methods

Two years old shea seedlings were subjected to simulated late burning which typically occur in the first quarter of the year with estimated mean flame temperatures between 235°C - 496°C (Kugbe, 2012). This was actualized by valuing the fuel load of the savanna reported as 2-3 t ha^{-1} in Ghana (Saarnak 1999) which was deduced to 76 g m^{-2} per pot area of 0,038 m^2 supposing 2 t ha^{-1} fuel load. Harvested grasses of *Cenchrus pedicellatus* were dried to constant weight and 76 g was placed in each pot with one shea seedling. Dry grass was ignited by naked fire using Bunsen burner flame (Labogaz 206, Campinggaz, Bristol, UK) and was completely burned down. 24 hours after fire all pots of the treatment and control were watered (n=6). Re-growth of the fire treated plants started two weeks after simulated fire. Shea seedlings were allowed to grow under the same conditions for 16 weeks after which measurements were taken.

Chlorophyll fluorescence measurements were taken on three separate occasions using the OJIP protocol with the chlorophyll flourometer (OS-30p, Oti-Sciences Inc. Hudson, USA) on the second and third leaves of the shea seedlings at actinic light pulse intensity of 3500 µmols after a dark adaptation of 30 min using dark adaptation clips. Three measurements on the two leaves per plant were averaged. Measurements were used to calculate the parameters of maximum quantum yield of photosystem II (Fv/Fm) and the performance index (PI). In addition three measurements of chlorophyll content and of the nitrogen balance index (NBI) of six leaves per shea seedling were taken using the chlorophyll meter (Force-A Dualex, Scientific+™A, Cedex, France).

Oven dried shea leaves and roots of all treatments were finely ground using a Retsch mixer mill (MM-400, Fischer Scientific, Suwanee, USA). Aliquots of oven dried samples (leaves and roots) were weighed into 4x6 mm tin cups (HEKAtech, Germany) for C and N content and C isotope determination in an isotope ratio mass spectrometer (nu Horizon, Nu Instruments Limited, UK) linked to an elemental analyzer (EURO-EA 3000, Euro Vector, Italy) in a continuous flow configuration (set-up by HEKAtech, Germany). Isotope and mass calibration was conducted by the use of the certified standards IAEA-600 Caffeine (δ13C = -27.771 ‰ VPDB, SD 0.043; $\delta^{15}N$ = +1.0‰ air N_2, SD 0.2‰), IAEA-NO-3 Potassium Nitrate ($\delta^{15}N$ = +4.7‰ air N_2, SD 0.2‰) and 2,5-bis (5-tert-butyl-2-benzoxazol-2-yl) thiophene (6.51% N; 72.52% C; HEKAtech, Germany), respectively. All statistical analyses were carried out using the software package SigmaPlot 13 (Systat-Software Inc., San Jose, Canada). The content of N in the chlorophyll was estimated by dividing the chlorophyll content by the N in dry leaves. The content of chlorophyll/N ratio, NBI, FV/Fm, PI, C/N and $\delta^{13}C$ parameters were analyzed by student t-test for significant difference between fire and control treatments. Results are presented as box-plots.

B.5.4 Results and discussion

The recorded temperature of fire in the pots ranged between 365-495 °C which falls within the natural range recorded by Kugbe (2012). The C/N ratios of both the leaves (not significant; P=0.42) and roots (P=0.008) of plants subjected to fire were higher than those of the control plants (Fig. 1). The higher C/N ratio recorded in both organs in fire treatments is probably due to defoliation induced nitrogen allocation to newly formed leaves and high root soluble carbon concentration (Bazot et al. 2005). This was also probably due to the loss of N in above ground parts as a result of burning. Consistently, the increased C/N ratio of roots of fire treatments is the result of the use of large quantities of N-based compounds for rapid growth and biomass allocation to above ground parts (Stem, leaves) after fire leaving the roots deficient in N and increasing the C/N ratio. Our hypothesis of a low N in all organs is confirmed with the higher C/N ratios recorded herein in leaves and roots.

The chlorophyll per N ratio of leaves was significantly higher by 14% (P=0.020) in fire treatments compared to control while the nitrogen balance index (NBI) of Shea seedlings subjected to burning were non significantly higher than the control by 6% (Fig. 1). The Chl/N ratio can be interpreted as a very rough approximation for (Calvin-cycle) enzymes per chlorophyll with higher Chl/N ratio indicating lower carboxylation capacity in comparison to photon energy conversion potential in the case of fire treatment. The NBI index points to the plant N-nutritional status (Cartelat et al. 2005) with a higher NBI index pointing to higher allocation of carbon to phenol production because of low N status of fire treatment. Both the carbon-nutrient balance (Coley et al. 1985) and the growth differentiation (Herms and Mattson 1992) hypothesis argue that plants allocate more carbon to phenol synthesis under low N availability. There are however, reports of higher chlorophyll content in burnt than control plants of *Quercus ilex* in the Mediterranean (Fleck et al. 1996).

The fire treatment seedlings recorded noticeable lower values in Fv/Fm and also in the performance index (PI), even though these differences were not statistically significant (Fig.1). Since Fv/Fm is a measure for the maximum efficiency at which light absorbed by PS II is used for photochemistry, the decrease in Fv/Fm (and also in PI) is indicative of slightly increased non-photochemical quenching processes (esp. dissipation of absorbed energy) and / or photo inactivation of PS II reaction centers (chronic photo inhibition) (Baker 2008; Kalaji et al. 2014). Dissipation and photo inhibition can arise when a reduced carboxylation capacity is limiting the utilization of excitones leading to an accumulation of excessive photon energy (Lu et al. 2017). Thus, in both observations, the higher chlorophyll/N ratio and the lowered Fv/Fm of leaves regrown after fire treatment, are suggestive that N deficiency in leaves limits the carboxylation capacity while the energy absorbance remains unchanged. The noticeable small but non-significant decrease in the measured fluorescence parameters points to N-reallocation pattern of shea which enables shea to maximize photosynthesis very close to a harming threshold which might be considered as a good recovery strategy of shea seedlings after fire.

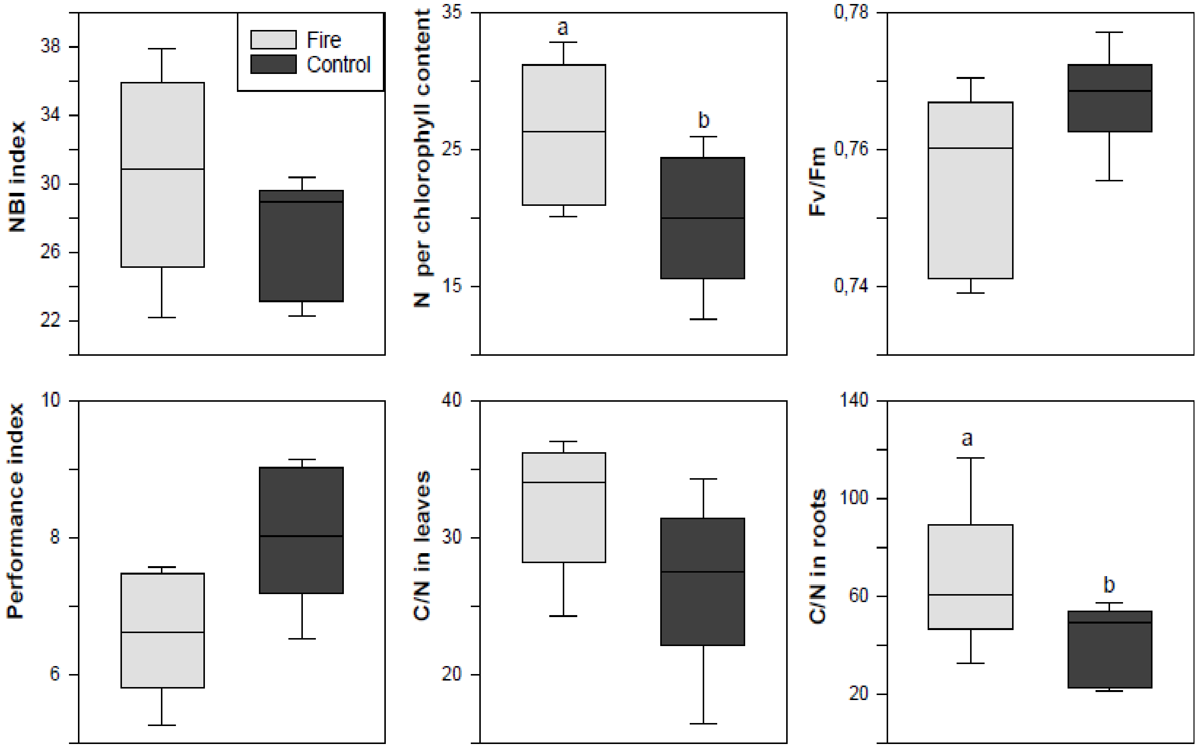

Fig. B.5.1 Differences in Chlorophyll content, fluorescence and C/N parameters between fire-treated and control plants. Different superscript indicate significant difference at p=0,005 with student t-test. n=6

The carbon isotopic signature (leaves) of the plants subjected to fire and control treatments were similar in leaves and also in roots (Fig. 2). This similarity was also reported after prescribed burning in Corsican and Ponderosa pine forest, respectively (Sala et al. 2005; Cannac et al. 2010). In post-fire Allepo pine however, $\delta^{13}C$ values were only significantly negative on wet sites but similar values were recorded on other sites (Alfaro-Sánchez et al. 2016). Nonetheless, a significantly higher $\delta^{13}C$ was reported in *Quercus ilex* after fire and also in resprouts after felling citing lower intercellular CO_2 (Fleck et al. 1996). Also a low relative conductivity resulting in higher water use efficiency and higher $\delta^{13}C$ were reported in *Pinus halepensis* after fire (Battipaglia et al. 2014). The similar $\delta^{13}C$ values reported here indicate an optimal fine-tuning of the CO_2 supply (stomatal conductance) to assumedly lowered CO_2 demand (carboxylation) of the newly formed and slightly N-deficient leaves.

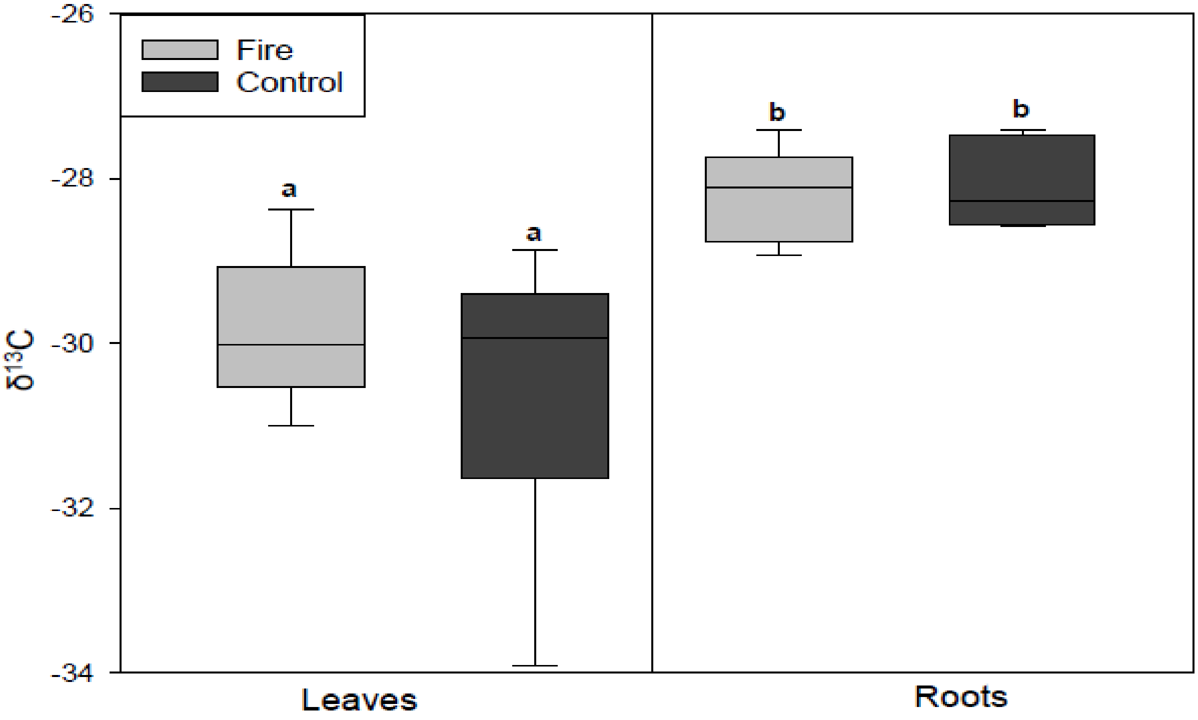

Fig.B.5.2. $\delta^{13}C$ in leaves and roots of fire-treated and control plants. Different superscript indicates significant difference at P=0,005 with student t-test. n=6

We recorded differences in $\delta^{13}C$ isotopes between leaves and roots in shea seedlings of fire and control treatments, with higher $\delta^{13}C$ in roots than in leaves of both treatments (Fig. 2). In the fire treatment, there was a 3% significant difference (P = 0.006) between $\delta^{13}C$ of roots and leaves while in the control treatment there was a 4% difference (P = 0.019). Opposite respiratory fractionation between leaves and roots has been a mostly cited reason for widespread differences between organ isotopic signatures because the CO_2 respired by leaves is enriched with $\delta^{13}C$ while that respired by roots is $\delta^{13}C$ depleted (Ghashghaie and Badeck 2014). Similar opposite $\delta^{13}C$ signatures of respired CO_2 from leaves and roots have been shown for the savanna tree species *Prosopis velutina* (Sun et al. 2012). There are also suggestions of further post-carboxylation fractionation as the cause of different organ carbon isotope signatures (Badeck et al. 2005). However, the relative increase of $\delta^{13}C$ in the roots of shea is in line with the hypothesis that dissimilar reactions result in CO_2 discriminating against the heavier $\delta^{13}C$ isotope.

In conclusion, shea seedlings exhibited impressive vitality after fire as displayed by the fluorescence parameters Fv/Fm and PI. The higher chlorophyll/N content in fire treatments confirms the low N availability after fire. However, the non-significant difference of $\delta^{13}C$ between the treatments in both leaves and roots are indicative of stomatal conductance and carboxylation potential to altered N-status of shea that recovered after fire. The nonsignificant increase in $\delta^{13}C$ in leaves of fire treated shea seedlings is a possible indicator of physiological adaptation of shea in response to environmental stress like fire.

B.5.5 **Acknowledgement**

We wish to express our profound gratitude to our greenhouse staff, Marion Klötzl and Maren Winnacker for their help in the greenhouse. We also acknowledge all the contributions and suggestions of Detlef Böhm.

CHAPTER SIX

6 THE EFFECTS OF GLOBAL CHANGE ON SHEA AND KYASUWA – A SYNTHESIS

This thesis focuses on the effects of global change drivers (CO_2, water availability, grass competition and fires) on shea and kyasuwa growth, biomass and nutritive value. The thesis also looks at mechanisms that have causal effects on shea and kysuwa growth. The results are presented in two parts; the first being a literature review of shea (chapter 2) and the second part of three chapters focusing on mechanisms that influence plant growth, biomass and nutritive value in response to global change. The results and methodological limitations have already been discussed. For brevity the majority of the results would not be repeated here. I intend to however, focus on the interactions of global change factors in eliciting plant responses in terms of photosynthesis, growth, biomass allocation, C and N allocation patterns and nutritive value.

6.1 Effects of global change on kyasuwa

The study on kyasuwa an important C4 grass in African savanna ecosystems, concentrated on how elevated CO_2, differences in water availability and in N-nutrition interact and affect growth and nutritive value of kyasuwa as illustrated in fig. 7.1.1.

Elevated CO_2 resulted in a decrease in stomatal conductance which in the case of kyasuwa did not translate into high water use efficiency. However, this rather occasioned a modification of the CO_2 influx to an apparently unchanged CO_2 demand thereby reflecting a similar assimilation potential as ambient CO_2 (Ghannoum et al. 2000). This was further manifest in the similar C/N ratio for both CO_2 treatments.

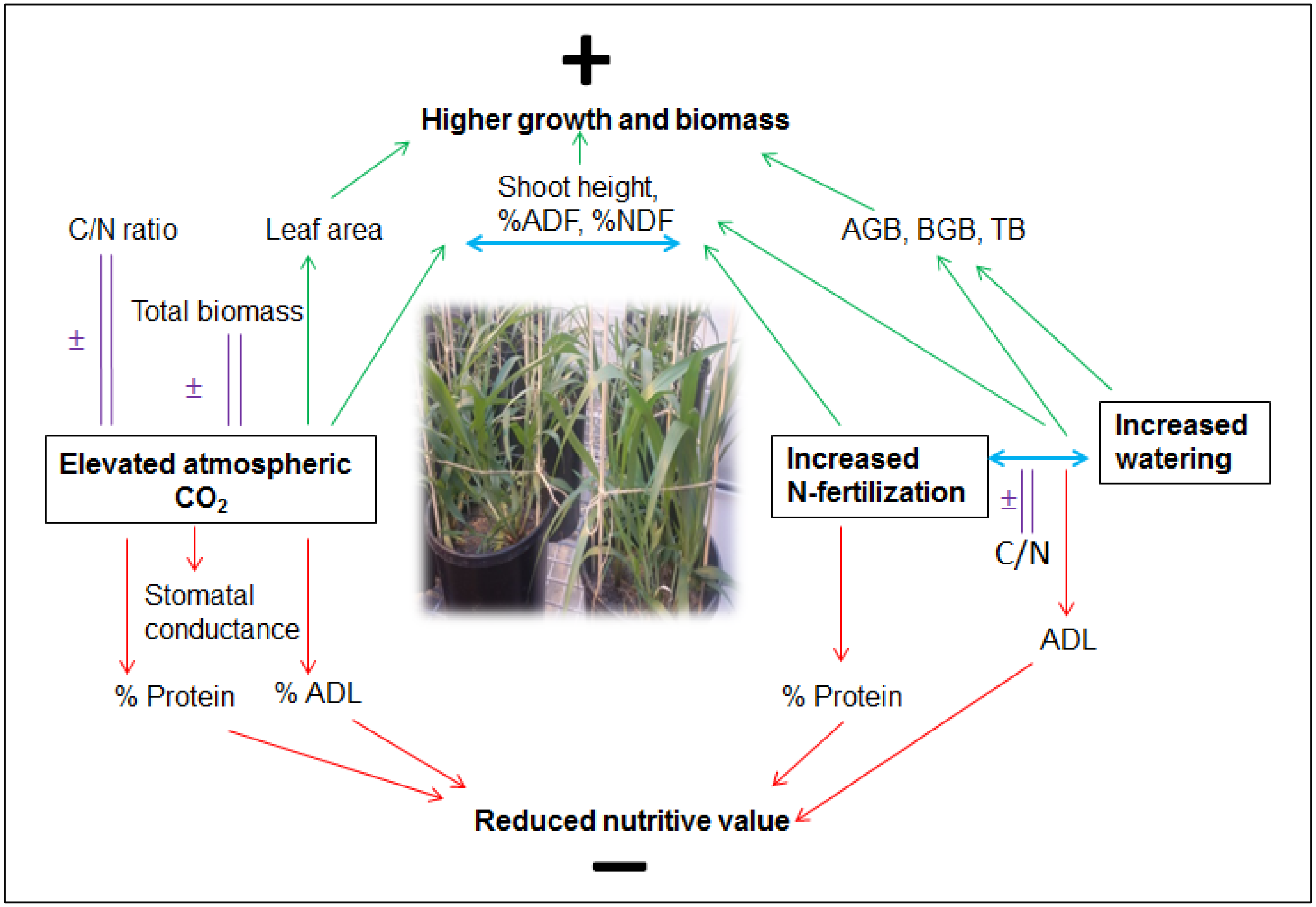

Fig. 7.1.1: Elevated CO_2, watering, and N-nutrition effects and interactions can either be positive (+), negative (-) or no effect change (±)

Interactive effects of watering regime and fertilization, however, resulted in decreased C/N ratios with N-fertilization only in low water treatments. This signifies the indirect effects of nutrient mobility. The future of kyasuwa under global change is unfavorable because eCO_2 leads to reduced root to shoot and generally reduced belowground biomass thus making kyasuwa less competitive in the savanna. Elevated CO_2 also reduced the protein content in kyasuwa without any interactive effect with the other factors. Reduction in protein content could probably be due to reallocation of N resources to other uses like to structural N-compounds or free amino acids thereby leaving a similar C/N ratio. Elevated CO_2 will result in changes in the chemical composition of kyasuwa with increases in structural carbohydrates (NDF and ADF) and reduction in ADL and protein which will reduce the nutritive value of kyasuwa overall.

The interactive effects of watering regime and fertilization on biomass accumulation and shoot height indicate that water supply is the most important limiting factor to kyasuwa growth. It is possible that kyasuwa fight drought stress for instance by investing in protective substances (e.g. LEA proteins, osmoprotectants and compartible solutes) and thereby produces less biomass during droughts (Schulze et al. 2005). However, in the long term, the reduction of stomatal conductance as a result of eCO_2 could cause increases in water use efficiency. Reich et al. (2018) recorded in a long term FACE experiments an interactive effect of water availability and eCO_2 with C4 grasses more responsive to eCO_2 in higher rainfall.

6.2 Shea and global change

6.2.1 *Effects of carbon dioxide, water availability and grass competition*

The main hypothesis of this thesis is that global change agents interact to elicit plant-trait responses and don't work in isolation as akin to the real world where several mitigating factors interact. Chapter four reports the interactive effects of global change factors CO_2, water availability and grass competition (Fig.7.2.1) on shea seedling growth.

Fig.7.2.1: Shea parkland with grass competing with shea

The light reactions of photosynthesis showed the maximum electron transport rate (J_{max}), the apparent quantum yield (ϕ), and the stomatal conductance (g_s) were differently affected by CO_2 concentration i.e. under low light (grass competition) and high light (no grass competition). We concluded that shea seedlings were adapted to low light conditions (shade) as created by tall grass or even older shea trees in parklands. We therefore agree with the hypothesis that light conditions (shade/light) have important effects on the relative impact of eCO_2 on carbon gain (Urban et al. 2014), which is in line with our hypothesis that global change factors interact to produce plant responses. Interactive effects of CO_2 on sun/shade leaves have been reported in *Quercus rubra* where growth response was significantly increased in shade under eCO_2 (Cavender-Bares et al. 2000). The responses of shea performance indicate interactive effects by the varied responses of shea as exposed to different global change scenarios (Fig.7.2.2).

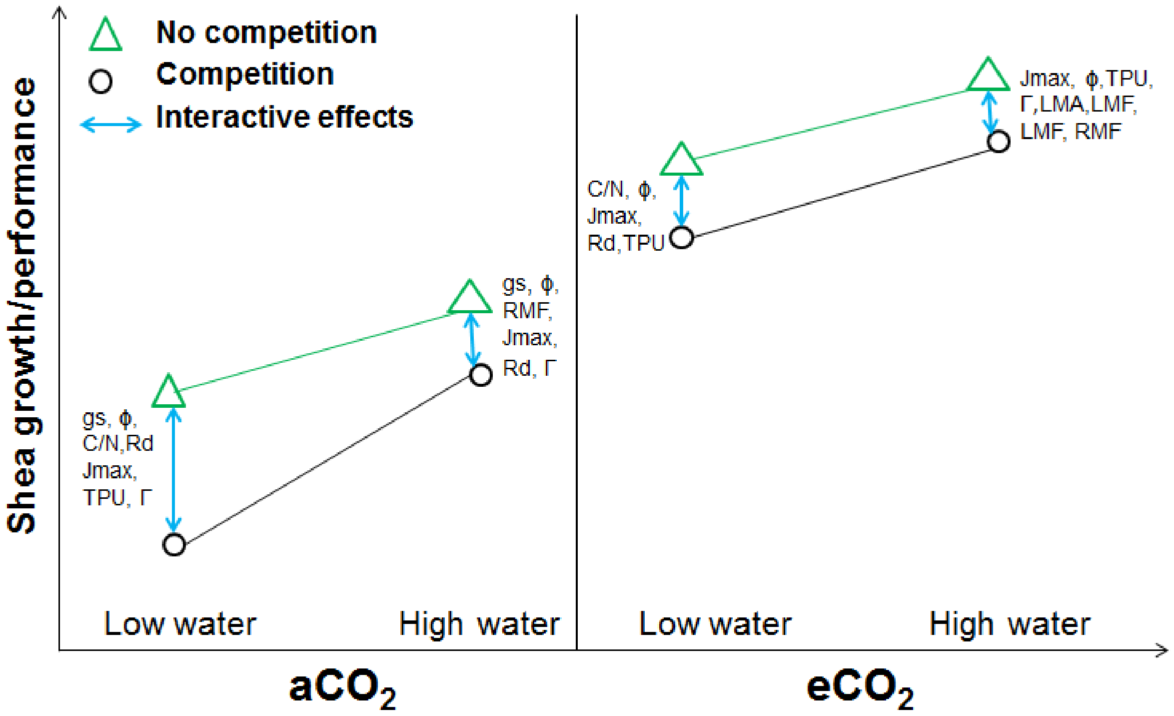

Fig.7.2.2: Model of shea responses to elevated CO_2, grown at low and high water availability and with or without competition showing interactive effects of factors.

Under ambient CO_2 and without grass competition, there was a decrease in shea performance under low water availability as a usual consequence of low water which results in reduced transpiration via decreased stomatal conductance and leads to reduced photosynthesis (Flexas 2002). However, also under ambient CO_2, the decrease in shea performance under low water availability becomes more pronounced with grass competition, since water resources will be even scarcer (Davis et al. 1999). These differential responses of shea under low water availability are a reflection of interactions of factors mimicking the occurrence in the savanna where several global change factors interact.

Elevated CO_2 is proven to lower stomatal conductivity at unchanged or even higher assimilation potential which results in a higher water use efficiency of C3 plants like e.g. shea (Ainsworth and Rogers 2007; Leakey et al. 2012). As a consequence in low water situations, there was an improved competitiveness against the C4 grass, since plants using the CO_2 concentrating C4 metabolism are reported to be less positively affected by eCO_2 than C3 plants regarding both assimilation potential and WUE (Wand et al. 1999; Ainsworth and Long 2004; Leakey et al. 2012). Nonetheless, where plants grow under water sufficiency, there was enough water available for shea seedlings even with grass competition and therefore a better performance of shea under eCO_2 was reported. However, the C4 grass although not affecting the shea, still stays strong since other resources become limiting in high water situations and elevated CO_2 favours species with high photosynthetic nitrogen use efficiency (C4 grasses) (e.g., Sage and Kubien 2003).

Overall, eCO_2 increased shea performance significantly especially when competing with C4 grasses under low water availability which clearly outlines the interaction of global change factors CO_2, water availability and grass competition. Higgins and Scheiter (2012) stressed the need to consider eco-physiological as well as demographic mechanisms to understand the effects of global change on the tree-grass interphase that make up savanna ecosystems. These mechanisms point to the interactive nature of global change factors in plant growth and dynamics in savanna ecosystems. In the future, although carbon dioxide will likely play a major role in shaping savanna ecosystems (Kgope et al. 2009; Buitenwerf et al. 2012; Bond and Midgley 2012; Higgins and Scheiter 2012), this will act together with other global change factors like rainfall, temperature and fire regimes. For instance, Higgins and Scheiter (2012) hypothesis alternative states (grasslands, savannas or forests) based on interactive effects of CO_2 and rainfall patterns. Shea responded to eCO_2 by increased allocation to the stem which may be important for seedlings to escape the next fire. However, the high water use efficiency under eCO_2 will aid shea during low rainfall periods, together with entrenched shea strategies to combat drought.

6.2.2 *Fire effects on shea*

Shea is reported to have outstanding attributes of recovery after disturbance (Hall et al. 1996; Nikiema and Umali 2007) and is therefore well adapted to the savanna ecosystem where fire is prevalent. This thesis suggests N reallocation as a mechanism behind this rapid recovery of shea after disturbances such as fire which leads to a total destruction of aboveground biomass. During fire, aboveground biomass is often partially/completely consumed leading to the volatilization of N in the aboveground parts as well the top soil. However, shea is known to strongly develop its root system after germination and establishes a root system before aboveground growth (Jackson 1974). Further to this, there are reports of a greater portion of shea seedling dry matter being located in the roots (Adomako 1985). Shea therefore has huge belowground resources as a pyrophytic species to enable it combat the hazards of savanna habitat that has long been subjected to annual burning (Jackson 1974). The hypothesis that fire consumes aboveground parts leading to loss and thereby resulting in low N in all shea parts was confirmed by the high C/N ratio in both the leaves and also in the roots of fire treatments. However the similar photosynthetic parameters which enabled comparable growth and biomass allocation highlight the physiological plasticity of shea. This thesis therefore suggests N resource reallocation and physiological plasticity as the mechanisms employed by shea in post-fire recovery.

6.3 Implications of global change on savannas

Future global change (especially eCO_2) looks unfavorable for kyasuwa growth making it less competitive with a reduced nutritive value in drought prone and infertile soils. Kyasuwa as a C4 grass inherently has a high water use efficiency, but the reduced stomatal conductance which was reported here did not further increase water use efficiency under global change. However, the biomass allocation towards a lower root to shoot ratio and a decrease in belowground biomass is worrisome for the survival of kyasuwa during long periods of drought. In parklands where grasses compete for resources with tree species like shea, it may be less competitive to tree seedlings which have more established belowground resources.

The implications of global change on shea parklands will be favorable to shea growth. Shea is reported to benefit from global change since it improves water use efficiency together with increased allocations to the stem and belowground biomass that could help shea seedlings escape the next fire. Shea is inherently resistant to drought by employing differential use of water resources dependent on availability/seasons (Bargués Tobella et al. 2017) and hydraulic redistribution (Bayala et al. 2008), however, eCO_2 causing an increased water use efficiency might even further benefit shea in the future. Secondly, increases in belowground biomass are also advantageous in cases of fire where there is total/partial combustion of aboveground biomass leading to losses in N-resources from aboveground parts. The increased belowground resources will come handy in such situations. Shea is therefore prepared for the challenges of global change since the improved WUE will help it to out-compete other plants species e.g. kyasuwa grass. Shea also employs physiological plasticity and resource reallocation in dealing with the annual fires that are characteristic of the parklands. This thesis therefore supports the hypothesis that eCO_2 will interact and influence trees growth positively compared to grasses (Kgope et al. 2009; Buitenwerf et al. 2012; Bond and Midgley 2012).

6.4 Perspectives for future research

The eco-physiological underpinnings of kyasuwa growth in future savanna ecosystems under global change are not clear from this study. Research in this regard will illicit mechanism employed by kyasuwa to combat future global change. Long term studies on kyasuwa are also required since long term FACE experiments of C3 and C4 grasses contradicted the current theory of C4 response to elevated carbon dioxide (Reich et al. 2018) as also reported in this thesis. The interactive effects of tree competition on kyasuwa growth and the possible mechanisms to challenge tree competition will possibly clarify the future distribution on savanna ecosystems.

Fire is a usual occurrence in shea parklands and an annual recurrence in the life cycle of shea, it would be important to investigate interactive effects of fire with other global change factors like eCO_2, water availability and even grass competition. Based on stable isotopes, Shanahan et al. (2016) indicate that the interactions between climate, CO_2 and fire can make tropical ecosystems more resilient to change. These interactive effects are especially crucial as fire resulted in a decrease in the amount of N in shea tissues and eCO_2 also increases C/N ratio. It will be important to investigate how fire will affect the interactive effects between CO_2 and water availability where C/N ratio is only increased in grass competition treatments with low water availability for both ambient and elevated CO_2. The interactive effects of fire and eCO_2 will improve our understanding of the different hypothesis reporting CO_2 to be the main driver of tree encroachment (Kgope et al. 2009; Bond and Midgley 2012; Higgins and Scheiter 2012) as opposed to prepositions that fire is responsible for keeping the open grassy state of savannas (Higgins et al. 2000; Bond et al. 2003; Prior et al. 2010). Long term studies on the interactions and effects of global change on shea are also required to better predict the future of shea parklands and the future sustainability of this important tree. Investigating the starch reserves of regrowth will better explain the plasticity of shea as well as ^{14}C labelling to trace the source of carbon used for post-fire regrowth. The higher WUE as a result of eCO_2 can be observed in the measurements of tree rings based on $\delta^{13}C$ measurements. Brienen et al. (2016) reported tree-ring studies to offer important insights to global change effects.

BOX 2

B.6.0 The future of growth rings in shea (*Vitellaria paradoxa* C.F.Gaertn.) research

Damian Tom-Dery, Anna Voggenreiter-Sandner, Christoph Reisdorff and Kai Jensen

B.6.1 Introduction

Dendrochronology is one of the most important environmental recording techniques for some natural environmental processes and a monitor for anthropogenic changes to the environment such as pollution and contamination (Speer 2010). The important foundation of dendrochronology is the presence of anatomically distinct, annual growth rings (Schweingruber et al. 1990). Tropical trees are known not to always reveal growth periodicity (and subsequent age) as clearly as their temperate counterparts by concentric changes in their wood anatomy (Gourlay 1995a; Worbes 2002).

Growth rings in tropical species are formed because of cambial dormancy that is controlled by the seasonality in moisture availability (Rozendaal and Zuidema 2011) with Gourlay (1995a) indicating ring formation occurring in the rainy season. Climatic fluctuations within the seasons in the tropics may lead however, to the formation of false rings (Priya and Bhat 1998), wedged rings (Worbes 2002), or even to a non-annual ring formation (Dünisch et al. 2003; Wils et al. 2009). Over the last decades, the annual character of tree rings has been established for a large number of species in many parts of Africa (e.g.Gourlay 1995b; Schongart et al. 2006; Steenkamp et al. 2008; Gebrekirstos et al. 2008, 2009, 2011; Wils et al. 2009; Fichtler et al. 2010; Nicolini et al. 2010; Mbow et al. 2013; van der Sleen et al. 2015; Colombaroli et al. 2016; Sanogo et al. 2016; Zacharias et al.

2018) thus providing a sound basis for applying tree-ring analysis to tackle ecological questions in African ecosystems.

Shea is a socially important species to the inhabitants of the areas where it grows and provides the cooking oil of about 86 million inhabitants (Naughton et al. 2014). The species generally thrives in the arid and semi-arid areas where annual rainfall amounts range between 400-1500 mm (Maydell 1990; Hall et al. 1996) and it tolerates an extended drought of up to eight months (Vermilye 2004). Annual leaf abscission occurs during the dry season and probably plays a major role in nutrient recycling through the decay of leaves and fine roots at the soil surface (Bayala et al. 2006). Shea has remarkable longevity reaching an age of up to 300 years (Delolme 1947; Ruyssen 1957; Jøker 2000) and with implications for long term carbon sequestration (Luedeling and Neufeldt 2012).

The enormous importance of shea and products of shea butter has resulted in tremendous research on shea culminating in noteworthy reviews in terms of opportunities and challenges for improvement (Boffa 2015), nutritional and chemical properties (Honfo et al. 2014) and current knowledge and research gaps (Tom-Dery et al. 2017). The later review recommended dendrochronological research as a way forward. However, till date authors are aware of only one published dendrochronology research on shea in Mali that reports shea as forming distinct growth ring boundaries with parkland trees not successfully cross-dating due to management operations like pruning (Sanogo et al. 2016). The main aim of this research is to confirm growth rings in shea from Ghana as a correlate of rainfall amount. We hypothesize that the long drought season (5-8 months without rainfall) leads to cambial dormancy and to tree ring formation in shea. We also aim to discuss possible applications of dendrochronology in future shea research.

B.6.2. Materials and methods

B.6.2.1 Study area

The study was carried out along a rainfall gradient of ecological zones in Ghana where there are six ecological zones (Fig. B.6.1); Sudan Savannah, Guinea Savannah, Transition forest, Semi-deciduous forest, High Rainforest and Coastal Savannah (Nuhu et al. 2012).

In Ghana, shea trees are found mainly in the interior Savannah with some populations in the forest-savanna transition (Yidana 2004). The samples were taken along a rainfall gradient from the transition forest (bimodal: two rainy seasons in a year) with the highest rainfall figures per annum to the sudan savanna (uni-modal: one rainy season in a year) with the lowest rainfall figures. In the transition forest (Sample point (SP 01)), the mean annual rainfall was 1241±34 mm with a mean annual temperature of 30 ±1 °C. In the guinea savanna zone two sampling points were enumerated with different rainfall amounts but identical temperature ranges. Sampling point (SP 02, Tamale) had a mean annual rainfall of 1088±33 mm and a mean annual temperatures of 32±2 °C while the sampling point 3 (SP 03, Navrongo) which is further north has annual rainfall figures of 977±29 mm and a mean temperature of 35±2 °C. In the Sudan savanna zone, sampling point 4 (SP 04, Bawku) has annual rainfall figures of 963±37 mm with a mean annual temperature of 38±3°C.

B.6.2.2 Tree sampling

Fruiting trees were harvested at breast height (DBH=1.3 m) and complete stem disc portions were used for dendrochronology as is recommended for tropical trees (Worbes 2002). A total of three stem discs were obtained in each of the regions illustrated in Fig. B. 6.1. A total of twelve trees were sampled along a rainfall gradient in Ghana. The vegetation classification is mainly based on rainfall (Fig. B. 6. 1).

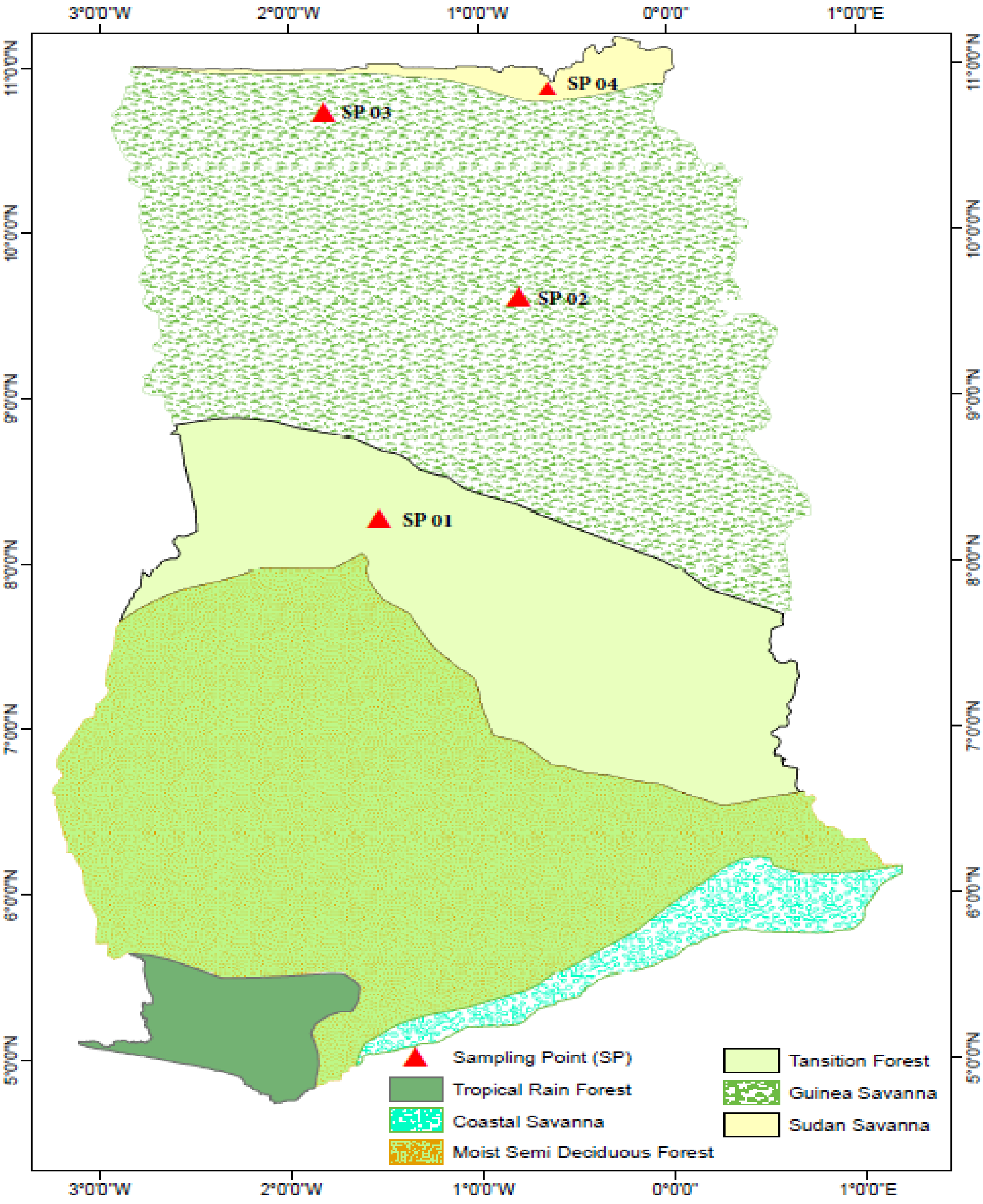

Fig. B.6.1 Vegetation map of Ghana illustrating sampling points (Source: Bernard Batuuwei)

B.6.2.3 Tree ring analysis

The stem discs of shea were dried under shade in an open area before being transported to the Dendrochronology laboratory of University of Hamburg. Standard dendrochronology methods were used in sample preparation for measurements (Cook et al. 1990). To enhance the visibility of growth ring boundaries, we polished samples gradually using a disc sander (RO 150, Festool, Indiana, USA) with grit sizes between 400-1000. Tree ring boundaries were marked under a microscope (Leica M80, Wetzle, Germany) coupled with a LINTAB^{TM} 6.0 measuring system (Rinntech Inc., Germany).Tree –ring widths were measured for two or three radii (from the bark to pith) to the nearest 0.01mm by means of LINTAB^{TM} 6.0 using TSAP-Win^{TM} (Time Series Analysis and Presentation, version4.64 for Microsoft windows: Rinn et al. 1996).

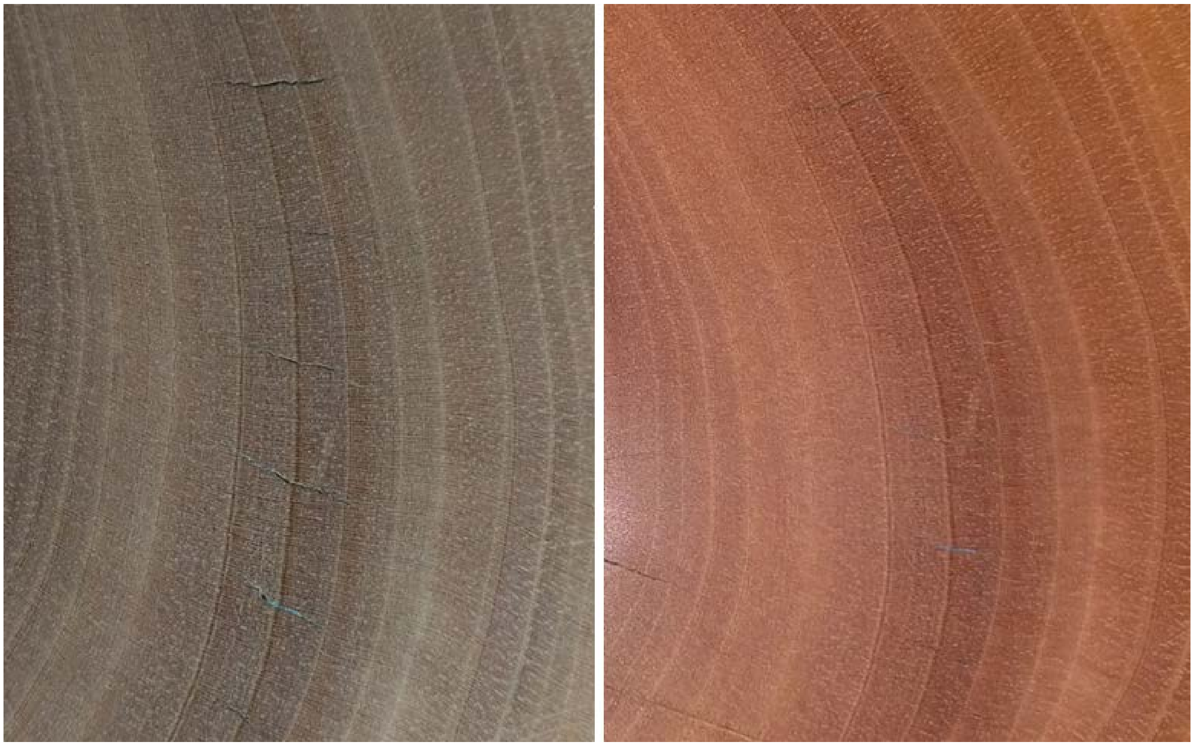

Fig. B.6.2 Images of growth rings in sample shea tree

Pointer years were used to detect and correct errors due to missing or false rings (Gebrekirstos et al. 2008). Statistically, cross-dating was verified using the software TSAP to measure *'Gleichläufigkeitkoeffizient'* (GLK: coefficient of parallel variation between tree-ring series) and T-value (a measure of significance in relation to the length of the overlap) that verifies the degree of similarity of two curves (Baillie and Pilcher 1973; Wigley et al. 1987). Series with GLK higher than 65% (Eckstein and Bauch 1969) and T-values greater than 2 were selected for further analysis. Using the same technique, successfully cross-dated mean ring width series of different sample trees were averaged to build vegetation zones chronologies.

B.6.3. Preliminary results

Shea has growth rings as shown in Fig. B.6.2 as also reported by Sanogo et al. (2016). However, there were false rings on some samples and the presence of partially indistinct rings. This makes cross-dating difficult and intensive. Nevertheless, the tree ring analyses revealed age ranges between 34 and 83 years. The sample size of 12 was, however, very small for making sound statistical comparisons. The chronologies of the various sampling points are presented in Fig. B.6.3.

B.6.4 Potential uses of tree rings in shea research

Confirming growths rings in shea has several important implications for future research on shea and shea parklands as well as the savanna ecosystem as a whole. Below are some future research perspectives.

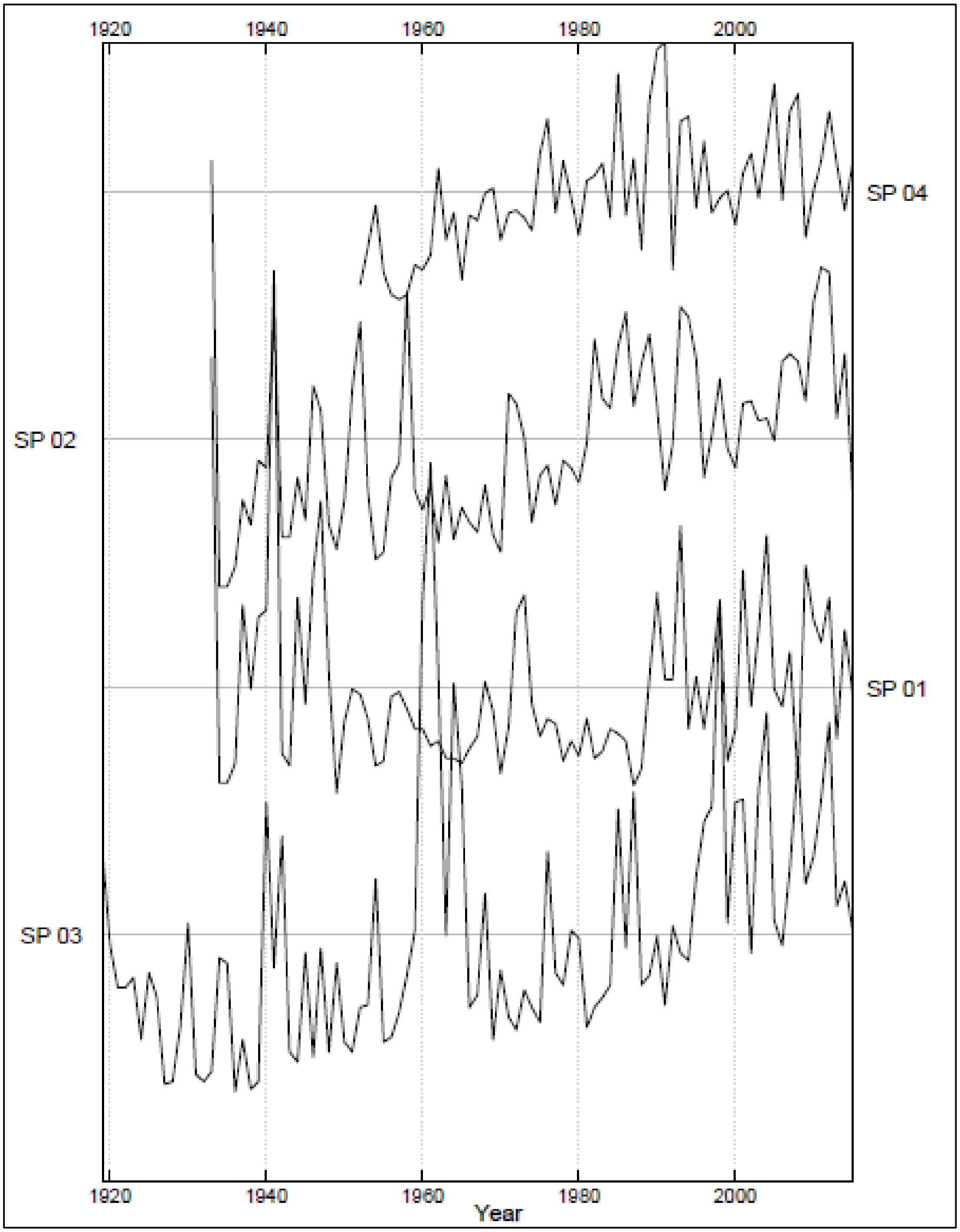

Fig. B.6.3 Chronologies of three trees per sampling points (SP) in the various zones

B.6.4.1 Age determination in shea

Shea is a long-lived tree species that is reported to grow up to 330 years (Delolme 1947; Ruyssen 1957; Jøker 2000). However, because shea is largely uncultivated, it is important to accurately determine its age scientifically. Dendrochronology offers a good opportunity to accurately determine the age of shea. Accurate age determination will enable future correlation of the age of shea trees to yield, possibly solving the issue of predicting the yield of shea thereby assuring a fairly constant supply of shea nuts for industries.

B.6.4.2 Analysis of fire history

Shea grows in parklands where fires are a recurring event annually. Bush fires cause changes in wood anatomy and growth that can be used to reconstruct fire histories (Swetnam 1993; Swetnam et al. 2009; Carroll et al. 2018; Rother et al. 2018). Understanding historical fire seasonality should facilitate development of concepts regarding fire as an ecological and evolutionary process (Rother et al. 2018). This could also provide important insights of the adaptations that shea as a pyrophytic species has used in these challenging periods of its life cycle.

B.6.4.3 Biomass and carbon sequestration estimation of shea

Although, growths rings in shea have been used to predict biomass (Sanogo et al. 2016), this was done using a generalized pantropical allometric model for dry forest. There is still a need for improvement to achieve exact biomass estimations. Initial shea specific allometric models presented 60% error for sites in Cameroon (Peltier et al. 2007). This model was also criticized for the few replicates of six samples used in the estimation. However, improved allometric equations for shea have recently been developed geared towards proper estimation of carbon sequestered by shea parklands. Allometric equations using DBH (Jibrin and Abdulkadir 2015; Dimobe et al. 2018) and also tree height (Dimobe et al. 2018) to predict aboveground biomass of shea now exist for Nigeria and Burkina Faso. Jibrin and Abdulkadir (2015) used 36 sample trees in their estimation and achieved a 6% error while (Dimobe et al. 2018) also with a relative high number of 30 sample trees recorded an equally low error of 7%. Therefore, carbon sequestration rates can now be accurately estimated with growth rings coupled with accurate allometric models.

B.6.4.4 Reconstruction of past climate

Most of the savanna ecosystems is located in Africa (Shorrocks 2007) where there is a scarcity of instrumental climate data leading to poorly understood drivers of climate, their interactions and impacts (Gebrekirstos et al. 2014). This would probably be important in cases where drought reconstruction to indicate past climate history is needed. Using shea tree rings, it is possible to precisely date high-resolution climate proxies recreating local climate variability. Appropriate use of a range past climate scenarios combined with analysis of trends in historic data can contribute to the understanding of future trends and uncertainties that are crucial for long-term planning perspectives (Eastaugh et al. 2010; Sanogo et al. 2016).

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Key Findings (Chapter 2-5)

- The review revealed the establishment of a harmonized methodology for determining the distribution, density, chemical and nutritional analysis as well as characterization of regional populations as timeously required. Research is needed on the eco-physiology of shea seedlings under current and projected climate scenarios and dendrochronology.
- Elevated CO_2 increased individual leaf area of kyasuwa thereby making it more attractive as forage and change in biomass allocation towards a lower root and shoot ratio, that may be harmful to the species in arid areas with low nutrient availability. There was an overall reduction in nutritive value of kyasuwa with eCO_2 while water and fertilization were the two most limiting resources compared to CO_2 and did not mostly interact with CO_2.
- Photosynthetic carbon uptake in shea seedlings was enhanced by eCO_2 while the stomatal conductance was reduced resulting in increased water use efficiency. Although there was no change in biomass, there was higher allocation to stems and an increased leaf area. On the contrary, grass competition resulted in a reduction of photosynthetic and dark respiratory rates; it also resulted in decreases in growth, reduced allocations to leaves and stems and all biomass parameters.
- Stimulated burning was a better way of mimicking savanna fires than the traditional methods. Similar rates of gas-exchange, growth, biomass parameters and $\delta^{13}C$ in both the leaves and roots were reported in both the burned and control treatments. Shea is able to recover rapidly after fires by employing resource reallocation and physiological plasticity.

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Author Contributions

Chapter 1	D. Tom-Dery wrote this chapter.
Chapter 2	D. Tom-Dery reviewed most of the literature and came up with the structure of the manuscript as well as wrote the initial draft.
Chapter 3	D. Tom-Dery conceived the idea, designed and set up the greenhouse experiment, conducted all measurements, lab analysis and analyzed all data (including statistics), and also wrote the initial draft of the manuscript.
Chapter 4	D. Tom-Dery conceived the idea, designed and set up of the experiment, conducted measurements in the greenhouse and lab analyses, analyzed all data (including statistics), and wrote the initial draft of the manuscript.
Chapter 5	D. Tom-Dery designed and set up the field study, conducted measurement and lab work, analyzed all data (including statistics), and wrote the initial manuscript.
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Chapter 6	D. Tom-Dery wrote this chapter. All findings are based on research and data analysis in chapters 2-5.
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Information on published chapters

Chapter 2

Shea (*Vitellaria paradoxa* C. F. Gaertn.) at the crossroads: Current knowledge and research gaps

Published in: *Agroforestry Systems*

Publisher: Springer

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DOI: 10.1007/s10457-017-0080-y

Authors: **Tom-Dery D**, Eller F, Reisdorff C, Jensen K

D. Tom-Dery reviewed most of the literature and came up with the structure of the manuscript as well as wrote the initial draft.

Signature

Prof. Dr. Kai Jensen (Supervisor)

Chapter 3

Effects of elevated carbon dioxide and climate change on biomass and nutritive value of Kyasuwa (*Cenchrus pedicellatus* Trin.)

Published in: ***Journal of Applied Botany and Food Science***

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Year: 2018

DOI**:** 10.5073/JABFQ.2018.091.012

Authors: **Tom-Dery D**, Eller F, Jensen K, Reisdorff C

D.Tom-Dery conceived the idea, designed and set up the greenhouse experiment, conducted all measurements, lab analysis and analyzed all data (including statistics), and also wrote the initial draft of the manuscript.

Signature

Prof. Dr. Kai Jensen (Supervisor)

Published chapters information

Chapter 4

Elevated CO_2 does not offset effects of competition and drought on growth of shea (*Vitellaria paradoxa* C.F. Gaertn.) seedlings

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Authors: **Tom-Dery D**, Eller F, Fromm J, Jensen K, Reisdorff C,

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Signature

Prof. Dr. Kai Jensen (Supervisor)

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October 22, 2018

To whom it may concern,

As a native English Speaker, I do hereby declare that the PhD thesis: “Global Change Effects on *Vitellaria paradoxa* (C.F. Gaertn.) and *Cenchrus pedicellatus* (Trin.)“ has been written in concise and correct English (US).

Sincerely,

Heather Alyson Shupe

Declaration

I hereby declare, on oath, that I have written the present dissertation by myself and have not used other than the acknowledged resources and aids referenced.

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

....

Hamburg, den 24/10/2018

Unterschrift (Damian Tom-Dery)