

**Sapling ecology and management in multi-species
afforestation system on degraded cropland in the
Sudano-Sahelian zone of Benin**

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"At least there is hope for a tree: If it is cut down, it will sprout again, and its
new shoots will not fail."

The Bible, Job 14:7

"The best time to plant a tree was 20 years ago. The second best time is now."

Chinese Proverb

ABSTRACT

Sub-Saharan Africa faces the multiple challenges of improving food security of the rapidly growing human population while halting the severe land degradation and coping with climate change impacts. Re- and afforestation of degraded lands have been recognized worldwide as cost-effective strategies to mitigate and adapt to adverse environmental changes. In this respect, the establishment phase of tree plantations is in particular decisive for the sustainability of forestation enterprises, since the early development determines long-term growth trajectories and potential yields. Through a combination of open-field experiments and modeling, this study aimed to improve the understanding of sapling eco-physiology and responses to silvicultural management of multipurpose tree species (MPTS) introduced on degraded cropland in the Sudano-Sahelian zone (SSZ) of Benin, West Africa.

Survival, above- and belowground functional traits and biomass production of five MPTS subjected to manuring (1 kg per sapling) and/or supplemental drip irrigation (0.5 L per sapling daily) were monitored over the first 15 months after planting, covering two rainy (growing) and one dry season. Based on the relative growth rates (RGRs) observed, species were classified as (i) fast-growing (*Leucaena leucocephala* Lam., *Jatropha curcas* L. and *Moringa oleifera* Lam.) or (ii) slow-growing (*Anacardium occidentale* L. and *P. biglobosa* Jacq.). All species successfully established on degraded cropland, albeit with differing survival rates (67-100%). The fast-growing species had the highest survival rates (94-100%). Dry-season irrigation resulted in a 10-fold reduction in the mortality of *P. biglobosa*, and fertilization consistently enhanced shoot growth in all species during the growing seasons. These management interventions had either insignificant or positive effects on root growth. However, belowground biomass allocation was mediated predominantly by ontogeny, which explained 86-95% of the variation in root-shoot biomass relationships.

Allometric equations based on sequential measurements of stem diameter and tree biomass (i.e., leaves, stems and roots) showed very good fits ($R^2 > 0.93$). Following the integration of these equations with field-collected climate and soil physico-chemical data in the Water, Nutrient and Light Capture in Agroforestry Systems model (WaNuLCAS), the early growth dynamics of *J. curcas* and *M. oleifera* were reproduced with acceptable accuracy and precision. Climate-growth analysis using historical climate data (1981-2016) revealed that drought (indicated by annual water deficit, length of the longest dry spell and length of the dry season), projected to increase in severity and occurrence in the SSZ, was the main climatic factor limiting sapling growth and thereby posing risks for future afforestation efforts. However, scenario analysis of rooting depth greater than the empirical values suggests that deeper rooting might be an effective adaptive trait to enhance biomass growth under extreme dry conditions, and thus reduce sapling sensitivity to drought.

Overall, all five MPTS were assessed as suitable for the afforestation of degraded cropland: the fast-growing species due to the high responsiveness of aboveground traits to silvicultural management during the rainy seasons, and the slow-growing species due to their ability to maintain growth during the dry season and to adjust to the prevailing water and nutrient stress through increased resource allocation to roots. Given the investment risks for smallholder farmers in the SSZ, the vast area of degraded croplands, and the projected increase in extreme weather events, an afforestation system that integrates silvicultural management and a diversity of species able to develop deep-penetrating root systems will have the highest potential to increase the resilience of tree plantations to the climate change and deliver expected benefits. The presented findings are relevant to local and regional decisions on land restoration and forest management in the SSZ, and might be of interest for other dryland agro-ecological zones.

Ökologie und Management von Jungbäumen unterschiedlicher Arten in Aufforstungssystemen auf degradierten Anbauflächen in der Sudan-Sahelzone in Benin

KURZFASSUNG

Subsahara-Afrika steht vor der vielfachen Herausforderung, die Ernährungssicherheit der schnell wachsenden Bevölkerung zu verbessern die voranschreitende Landdegradierung einzudämmen und gleichzeitig mit den Auswirkungen des Klimawandels umzugehen. Die (Wieder-)Aufforstung degradierter Böden ist in diesem Zusammenhang weltweit als kosteneffiziente Strategie anerkannt, die eine Anpassung an negative Umweltveränderung erleichtert und deren Auswirkung mindert. Dabei ist die Anpflanzungsphase für die Nachhaltigkeit der Aufforstungsvorhaben entscheidend, da in der frühen Entwicklung langfristige Wachstumsverläufe und Ertragspotenziale bestimmt werden. Durch die Kombination von Freifeldversuchen und Modellierung, versucht diese Studie das Verständnis der Ökophysiologie von Jungbäumen und der Reaktion von Mehrzweckbaumarten (MPTS) auf forstwirtschaftliches Management auf degradierten Anbauflächen in der Sudan-Sahelzone (SSZ) in Benin (Westafrika) zu verbessern.

Es wurden in dieser Studie fünf MPTS in den ersten 15 Monaten nach der Pflanzung beobachtet. Forstwirtschaftliches Management beinhaltete Düngung (1 kg pro Schössling) und/oder ergänzende Tropfbewässerung (täglich 0,5 l pro Jungbaum). Der Untersuchungszeitraum umfasste zwei Regen- (Wachstumsphasen) und eine Trockenzeit. Im Beobachtungszeitraum wurden die Überlebensrate, sowie ober- und unterirdische funktionelle Merkmale und Biomasseproduktion ermittelt. Basierend auf den beobachteten relativen Wachstumsraten (RGRs) wurden die Arten als (i) schnell wachsend (*Leucaena leucocephala* Lam., *Jatropha curcas* L. und *Moringa oleifera* Lam.) oder (ii) langsam wachsend (*Anacardium occidentale* L. und *P. biglobosa* Jacq.) klassifiziert. Alle Arten wurden erfolgreich auf degradierten Anbauflächen angepflanzt, allerdings mit unterschiedlichen Überlebensraten (67-100%). Die schnell wachsenden Arten hatten die höchsten Überlebensraten (94-100%). Bewässerung während der Trockenzeit führte zu einer zehnfachen Verringerung der Sterberate von *P. biglobosa* und Düngung erhöhte das Triebwachstum aller Arten in den Wachstumsperioden. Beide Maßnahmen hatten positive Auswirkungen auf das Wurzelwachstum, dennoch konnte 86-95% der Variation im Wurzel-Spross Biomasseverhältnis durch Ontogenese erklärt werden.

Basierend auf wiederholten Messungen des Stammdurchmessers und der Baumbiomasse (d.h. Blätter, Stämme und Wurzeln) wurden allometrische Gleichungen entwickelt, die sehr gute Anpassungen zeigten ($R^2 > 0,93$). Nach der Integration dieser Gleichungen, samt der im Feld erhobenen Klima- und bodenphysikalisch-chemischen Daten, in ein Wasser-, Nährstoff- und Lichteinfang erfassendes Agroforstsystem-Modell (WaNuLCAS), wurde die frühe Wachstumsdynamik von *J. curcas* und *M. oleifera* mit akzeptabler Genauigkeit und Präzision reproduziert. Eine Klimawachstumsanalyse unter Verwendung historischer Klimadaten (1981-2016) zeigt darüber hinaus, dass Trockenheit (gemessen am jährlichen Wasserdefizit, der Länge der längsten Trockenperiode und der Dauer der Trockenzeit), die in der SSZ an Häufigkeit und Schwere zunahm, der klimatisch wichtigste Faktor war. Trockenheit hemmt generell das Wachstum von Jungbäumen und gefährdet damit zukünftige Aufforstungsmaßnahmen. Eine Szenarioanalyse bei welcher die Wurzeltiefe größer ist als Erfahrungswerte nahelegen, deutet darauf hin, dass eine tiefere Bewurzelung ein effektives adaptives Merkmal zur Verbesserung des Biomassewachstums unter extremen

Trockenbedingungen sein könnte und somit die Empfindlichkeit von Jungbäumen gegenüber Trockenheit reduzieren könnte.

Insgesamt wurden alle fünf MPTS als geeignet für die Aufforstung degradierter Anbauflächen eingestuft: die schnell wachsenden Arten aufgrund der hohen Reaktionsfähigkeit ihrer oberirdischen Merkmale auf forstwirtschaftliches Management während der Regenzeit; die langsam wachsenden Arten aufgrund ihrer Fähigkeit, ihr Wachstum während der Trockenzeit aufrechtzuerhalten, indem sie durch erhöhtem Wurzelwachstum Wasser- und Nährstoffarmut begegnen. Angesichts des Investitionsrisikos für Kleinbauern in der SSZ, den großen Flächen degradierten Ackerlandes und des prognostizierten Anstiegs von Extremwetterereignissen sind Aufforstungssysteme empfehlenswert, die das Anpflanzen von tiefwurzelnden Arten und forstwirtschaftlichem Management kombinieren. Auf diese Art kann das größte Potential erreicht werden, widerstandsfähige Baumplantagen zu etablieren, die dem prognostizierten Klimawandel standhalten und den erwarteten Nutzen erzielen. Die vorgestellten Ergebnisse sind insbesondere für lokale und regionale Entscheidungen mit Bezug auf die Rehabilitation von degradierten Böden und die Bewirtschaftung von Aufforstungssystemen in der SSZ relevant. Auch für andere agroökologische Zonen in Trockengebieten sind die Ergebnisse von Interesse sein.

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ACRONYMS AND ABBREVIATIONS

A/R	Afforestation/Reforestation
AGB	Aboveground biomass
ATWP	Annual total wet-day precipitation
AWD	Annual water deficit
BD	Bulk density
BGB	Belowground biomass
C	Control treatment
C	Carbon
CEC	Cation Exchange Capacity
CDM	Clean Development Mechanism
CO ₂	Carbon dioxide
D	Diameter at stem base
F	Fertilization treatment
FEM	Functional equilibrium model
H	Height
I	Irrigation treatment
IF	Irrigation plus fertilization treatment
K	Potassium
Ksat	Saturated hydraulic conductivity
LDN	Land degradation neutrality
LDS	Length of dry season
LDSP	Length of the longest dry spell
MaP	Month after planting
MAPE	Mean absolute percentage error
MPTS	Multipurpose tree species
MRE	Mean relative error
N	Nitrogen
OM	Organic matter
OPT	Optimal partitioning theory
P	Phosphorus
REDD +	Reducing emissions from deforestation and forest degradation, as well as conservation, sustainable management of forests and enhancement of forest carbon stocks
RGR	Relative growth rate
RSR	Root–shoot ratio
SDG	Sustainable Development Goal
SSA	Sub-Saharan Africa
SZZ	Sudano-Sahelian zone
WASCAL	West African Science Service Center on Climate Change and Adapted Land Use (WASCAL) program

1 GENERAL INTRODUCTION

1.1 Problem setting

In recent decades, concerns about the on-going land degradation¹ have increased as the global demands for food, feed and fuel continue to rise, while the share of productive agricultural land is shrinking in many parts of the world (Gelfand et al. 2013; Lambin et al. 2013; Gibbs and Salmon 2015; FAO 2017). Sub-Saharan Africa (SSA), a region with the highest rate of poverty in the world and where the majority of the population derives its livelihoods from subsistence agriculture, has experienced the most severe land degradation (Nkonya et al. 2016). With a rapidly growing population, the pressure on the land-resource base is intensifying in the region. The high levels of poverty in SSA coupled with the increasing rate of cropland degradation constitute a serious threat to food security, environmental health and rural livelihoods, particularly in the (semi-)arid regions such as the Sudano-Sahelian zone (SSZ) (e.g., Eswaran et al. 2001; Bai et al. 2008).

The semi-arid SSZ is a land strip spanning from Senegal in the west to Djibouti and Somalia in the east and located between the Sahara desert as the northern border and the humid Guinean zone as the southern border (Appendix A1). This zone has been an area of global concern since the early 1970s and 1980s, triggered by several severe droughts, associated land degradation and desertification (Tucker and Nicholson 1999). Extensive population growth, inappropriate land management and strong climatic fluctuations are reportedly the major drivers of the degradation of agricultural and forest lands (Herrmann and Hutchinson 2005; Karlson and Ostwald 2016).

The expansion of cropland to feed the rapidly growing population in the SSZ comes at the cost of reduced carbon stocks in natural vegetation and soil organic matter (e.g., Post and Kwon 2000; West et al. 2010; Vlek et al. 2017). The inherent low soil fertility and the permanent removal of nutrients from the agricultural systems have already resulted in severe soil nutrient mining in the SSZ (Stoorvogel and Smaling 1990;

¹ Land degradation sets in when land loses its intrinsic qualities or capability to perform vital ecological and economic functions (Katyal and Vlek 2000; MEA 2005)

Bationo et al. 1998). The use of organic and/or inorganic fertilizers to replenish minerals and nutrients in cultivated soils is socio-economically barely feasible (Lamers et al. 2015a, b) because of high prices, poor enabling policies, and risks of crop failure due to drought (Bationo et al. 2012). In the absence of appropriate land management, cropland degradation is therefore unavoidable, eventually leading to land abandonment.

The semi-arid SSZ is characterized by a high climatic variability manifested by large spatio-temporal fluctuations in rainfall levels and extreme weather events that cause severe droughts and devastating floods (Nicholson 2001; Tschakert et al. 2010). These environmental risks are likely to intensify due to climate change predicted for the region (e.g., Ringler et al. 2010). The combined effects of low economic development, rapid population increase, unsustainable land management practices and climate change and variability will further exacerbate the fragility of the agricultural systems and add to the pressure on croplands. Among the low-cost land rehabilitation options that remain viable in the face of climate change, afforestation of degraded landscape segments is able to meet these challenges if it is tailored to local agro-ecological settings (Garrity et al. 2010).

1.2 Afforestation of degraded cropland and its relevance for the SSZ of Benin

In recognition of the importance of land restoration, several global initiatives such as the Bonn Challenge² and the Sustainable Development Goals (SDGs), in particular the SDG 15³, have emerged to support mitigation efforts. Target 2 of the SDG 15 is one of the most important agendas recognizing the importance of afforestation and reforestation (A/R) by aiming at substantially increasing global A/R by 2020. In addition, A/R projects have been promoted under REDD+ and CDM for combatting land degradation and offsetting carbon dioxide (CO₂) emissions (UNFCCC 1997, 2010).

²The Bonn Challenge, launched in September 2011, is a global effort to restore 150 million ha of the world's deforested and degraded land by 2020, and 350 million ha by 2030 (Source: <http://www.bonnchallenge.org/content/challenge>).

³The SDG 15 aims to "Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss."

The growing interest in restoring degraded croplands using afforestation is rooted in the demonstrated ability of tree-based land-use systems to increase agroecosystem resilience and rural livelihoods (e.g., Garrity et al. 2010). Deep rooting characteristics of suitable candidate species allow exploiting a large soil volume to satisfy nutrient and water demands and maintain production under water- and nutrient-stressed conditions. Tree-based systems can be self-sufficient in nitrogen (N) nutrition through N₂-fixation, and may enhance depleted soil nutrient stocks commonly observed in the SSZ of Benin. Such systems can generate high quantities of organic matter which, as soil surface residues, improve soil structure and water infiltration, and enhance carbon storage above- and belowground (Garrity et al. 2010; Khamzina et al. 2012). Food, fodder, fuel, fiber, bioenergy feedstock and income from timber and non-timber products are potential socio-economic benefits of tree-based farming systems (Garrity et al. 2010; Khamzina et al. 2012; Baumert et al. 2018) that could motivate the farmers to embark on the pathway of afforestation. The evidence together indicates that with appropriately selected species and silvicultural management approaches, the conversion of degraded croplands to tree plantations can yield higher returns than the continuous cropping of degraded lands where yield levels do not justify investments (e.g., Djanibekov and Khamzina 2016). To assess the potential of afforestation of degraded croplands for combatting the land degradation and increasing agroecosystem resilience to climate change in the SSZ of Benin, several research aspects were identified.

1.3 Research needs

Practical recommendations regarding the choice of tree species for the afforestation of degraded croplands and suitable silvicultural management options should rely on accurate assessments of the viability and growth potential of the species, starting at the early stages of growth. Seedling establishment and sapling growth represent the most critical phase of the life cycle of any perennial plant, during which water and nutrient deficiencies characteristic for degraded lands may cause mortality or compromise future performance (e.g., Sanchez-Gomez et al. 2008; Reubens et al. 2009). Available evidence shows that the afforestation of degraded croplands, a risky endeavor, must be preceded

by a comprehensive selection of the promising candidate species based on a thorough screening of eco-physiological characteristics (e.g., Lamers et al. 2006; Khamzina et al. 2012). Nonetheless, silvicultural measures to enhance or support early stages of growth are seldom considered in afforestation strategies (Khurana and Singh 2004), and seedling and/or sapling (auto-)ecology of promising woody species remains poorly understood (Bunker and Carson 2005; Reubens 2010). Such information has not been documented for the semi-arid SSZ of Benin, necessitating empirical research into key growth features, in particular plant functional traits, resource-use strategies and phenotypic plasticity in the context of afforestation of degraded drylands.

In response to environmental stressors, plants adjust biomass allocation depending on the most limiting resource as postulated by the optimal partitioning theory (OPT), sometimes also referred to as functional equilibrium model (FEM) (Brouwer 1963; Bloom et al. 1985). In nutrient-poor and drought-prone environments, roots play an essential role in the acquisition of soil-based resources, i.e. mainly water and nutrients. Understanding patterns of resource partitioning between above- and belowground would increase knowledge on tree responses to silvicultural management and facilitate the selection of appropriate species for planting on degraded croplands. However, studies on biomass allocation in the particular context of afforestation of degraded cropland are missing for the SSZ of Benin, primarily because plant establishment and sampling are challenging in open-field forestry experiments (e.g., Robinson 2004).

Determination of allometric relationships between biomass and stem diameter could facilitate non-destructive biomass estimations and alleviate efforts associated with repeated field biomass sampling (Brown et al. 1989). The information about the allometry of promising afforestation and agroforestry species specific for juvenile growth stage of trees remains to be documented for semi-arid Africa particularly because growth trajectories of trees introduced on degraded cropland differ from those of the same species under more favorable edaphic conditions. Realistic projections for biomass and carbon sequestration are therefore difficult, but are key in assessing the mitigation potential of young plantation forests (e.g., Baumert et al. 2018).

Global warming necessitates the assessment of impacts of climate change and variability on tree growth and the development on this basis of appropriate adaptation strategies. However, the effects of increases in rainfall variability and temperature on the early growth dynamics of trees have received little attention in general and none at all for woody species in the SSZ of Benin. Yet such knowledge would be of major interest to land-use planning and sustainable management of forests and tree plantations (e.g., Comita and Engelbrecht 2014). Field experiments aiming for such assessments remain rare and are often costly because the existing complexities in soil–plant–climate interactions may necessitate repeated field trials under various climatic and edaphic conditions. Available methods such as dendrochronology frequently used to analyze climate–growth relationships may not be suitable for assessing climate risks in the early stages of tree growth due to the problematic features of wood anatomy such as missing, discontinuous and false rings common in tropical species (Brienen and Zuidema, 2006; Herrera-Ramirez et al. 2017).

To ease some of these challenges, early indicators of long-term growth potential and performance of woody species such as the relative growth rate (RGR) should be considered (e.g., Shipley 2000; Lamers et al. 2006). Moreover, field experiments could be complemented with additional assessment methods such as process-based modeling of tree growth (e.g., van Noordwijk and Lusiana 1999; Luedeling et al. 2016) to integrate available empirical data and broaden the site-specific results of field experiments using scenario analysis of climate change impacts on early plant growth and of possible physiological adaptations. A combination of these approaches can support better-informed decisions on the selection of tree species and silvicultural management for current and future afforestation projects.

1.4 Research objectives and structure of the thesis

The overarching goal of this study was to improve the understanding of the process of (re-) establishing tree cover on degraded cropland in the SSZ of Benin under the prevailing environmental stresses and silvicultural interventions. The research findings on eco-physiology and responses of promising tree species to management are

expected to support decision-making regarding the restoration of the productivity of degraded croplands in dry areas through afforestation. In the long term, this may contribute to climate change mitigation and improve rural livelihoods in the SSZ of Benin and beyond.

The specific research objectives were to assess:

1. Survival and early growth responses of five MPTS grown on degraded cropland and subjected to supplemental irrigation and manure application, focused on in Noulèkoun et al. (2017a);
2. Effects of resource availability and ontogeny on biomass production and allocation in the five MPTS, targeted in Noulèkoun et al. (2017b);
3. Sapling biomass allometry and potential for carbon sequestration of the five MPTS, addressed in Noulèkoun et al. (2018a);
4. Climate sensitivity of selected MPTS in the early stages of the tree plantation development on degraded cropland, focused on in Noulèkoun et al. (2018b).

This thesis is presented as a compilation of four scientific articles (Noulèkoun et al. 2017a, b, 2018a, b) published in international peer-reviewed journals included in the Science Citation Index (SCI). The thesis summary comprises a general introduction (Chapter 1), an overview of methodologies employed in the study (Chapter 2), key scientific findings and discussion of their contribution to general knowledge of tree eco-physiology and management (Chapter 3), and general conclusions and implications of the findings for further research (Chapter 4). Following are literature references and additional materials included as separate items (Appendix A). The journal articles in their published form along with related supplementary information are presented in Appendix B.

1.5 Description of the study area

1.5.1 Location and demography

The semi-arid Atacora region in north-western Benin (1° 00' and 2° 00' E and 10° 40' and 11° 28' N), located on the Sudano-Sahelian belt (Appendices A1 and A2), was selected as the study area. Being part of the SSZ, Atacora is likewise exposed to land degradation driven by deforestation and soil nutrient mining (Adegbidi et al. 1999; Mulder 2000), which threaten the sustainability of farming systems and exacerbate rural poverty (Saïdou et al. 2004; Wala 2005). The study was carried out in Pouri village in the commune of Matéri, which is one of the nine communes in the Atacora region (Appendix A2). In Matéri, one of the three study sites (Dassari Basin) of the WASCAL⁴ program is located. The Atacora region has a high population growth rate (3.02% between 2002 and 2013; INSAE 2013). About 68% of the population lives in rural areas, and agriculture and animal husbandry are the main livelihood sources (INSAE 2013).

1.5.2 Climate and soils

The climate is semi-arid, characterized by one rainy season (usually from April to October) and one dry season (usually from November to March) (Figure 1 in Noulèkoun et al. 2018b). The dry season is marked in the first months by strong, dry, north-east winds locally called “Harmattan”, originating in the Sahara Desert. The annual precipitation between 1981 and 2016 ranged from 674-1509 mm, underlining a high inter-annual variability, which is likely to increase due to climate change. Moreover, the inter-seasonal variability is subject to large variations (Sylla et al. 2016a, b). The long-term (1981-2016) mean annual air temperature is 27.5°C (Figure 1 in Noulèkoun et al. 2018b), while absolute daily minimum and maximum temperatures may reach 11°C and 45°C, respectively. These temperatures are predicted to increase under future climate conditions. The projected changes in rainfall patterns and temperature for the region will likely influence the growth and productivity of crops and trees.

The region is characterized by fersialitic and ferralitic soils with low to moderate inherent fertility and poor water holding capacity (Bationo et al. 1998; Azuka

⁴ West African Science Service Center on Climate Change and Adapted Land Use; <http://www.wascal.org/>

et al. 2015). Generally, the soils are shallow, crusted, compacted and limited in depth by gravelly or plinthic horizons (Saïdou et al. 2004). Because of the orographic influence on the topography, the soils are susceptible to *Harmattan*-driven wind erosion during the dry season (Röhrig 2008), while projected high rainfall intensities are likely to intensify water erosion during the rainy season.

1.5.3 Land use and land cover

The main land-use types in the region include agricultural lands (i.e., croplands, grazing lands, irrigated lands and fallows), forests (i.e., natural and planted forests) and settlements.

Agriculture is of the subsistence type, mainly rainfed and predominantly oriented towards the cultivation of sorghum (*Sorghum bicolor* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), cowpea (*Vigna unguiculata* L.) and yam (*Dioscorea* spp.) for household consumption. Cotton (*Gossypium* spp.) and, to a lesser extent, tobacco (*Nicotiana tabacum* L.) are principal cash crops. The practice of irrigation is in its infancy with only 0.27% of total agricultural land classified as irrigated land in 2008 (World Bank 2008). Farms are generally small and subjected to strong cropping pressure, leading to soil fertility decline (Callo-Concha et al. 2012). Crop production particularly suffers from low capital inputs (e.g., low use of external inputs such as chemical fertilizers, organic amendments, improved seeds, etc.) and environmental constraints (i.e., drought). Consequently, yields are generally low (Igué et al. 2000; Röhrig 2008) and are expected to continue to decline due to the projected increase in climate variability and the adverse effects on crop yields (Sylla et al. 2016a). Overall, the low agricultural productivity hinders reaching food security and poverty alleviation in the region.

The natural woody vegetation in the Atacora region consists of forests, and shrub and tree savannas dominated by *Parkia biglobosa* (Jacq.), *Isobertinia doka* Craib & Stapf, *Pterocarpus erinaceus* Poir. and other tree species (Wala 2005; MEHU 2011). According to the Benin forestry legislation (Law No. 93-009 of 2nd July 1993 on the establishment of forests in Benin Republic), the national forest area is subdivided into classified areas with restricted user rights and state-protected areas (MEHU 2011). The

Pendjari National Park, two hunting zones (Pendjari and Atacora), and the reforestation area of Natitingou (203 ha), all belonging to the classified forests areas, are located in the Atacora region. Despite this prime attention to conserve forest resources, the country lost about 13% of its natural forest cover between 1990 and 2015 at an annual deforestation rate of 1.2% (FAO 2015).

The main driver of this land-use change is the conversion of forests and tree savannas to agricultural lands. For instance, a recent study of the land-use and land-cover change in the Dassari Basin in the Atacora region reported an annual rate of loss in forest areas of 1.5% and a gain in agricultural lands of 1.8% between 2001 and 2013 (Chabi 2016). Obviously, the large-scale, national reforestation and forest enrichment programs initiated in the 1940s (FAO 2001) and in 2013 (<http://news.acotonou.com/h/61311.html>) were not able to counterbalance the loss in forest areas and fulfill the increasing demand for timber and non-timber products of the rapidly growing population. As such, there is much scope for the introduction and use of MPTs to restore degraded lands as well as for the development of appropriate silvicultural options towards successful A/R planning and implementation.

2 MATERIALS AND METHODS

2.1 Study sites

A cropping site at Pouri village (N 10°54'8.4" and E 1°4'47.4", altitude 186 m.a.s.l), devoid of tree cover and characterized by a declined productivity, was selected for setting up the multi-species afforestation trial (Appendix A2). The key selection criteria included (i) land-use history, (ii) land impoverishment (judged by nutrient stocks and crop yields), (iii) homogeneity in site conditions, (iv) site accessibility for regular field measurements, (v) presence of natural fallow land in the vicinity of the cropland to compare the productivity levels between afforestation and natural succession, and (vi) willingness of the land owner to allocate cropland for afforestation (Noulèkoun et al. 2017a). The selection of the site was preceded by a reconnaissance survey in the study area, which involved international and local forestry experts as well as local communities. The selected cropland was originally a savanna forest converted to agricultural land about 10 years prior to the experiment (Appendix A3). The soil at the site is an epipetric plinthosol (WRB, 2006) characterized by a sandy-loam texture in surface layers and clayey loam in deeper layers. At the onset of the experiment, the soil was acidic (pH 5.5), limited at the depth of 50 cm by a lateritic concretion, and characterized by low water holding capacity and low concentrations of macronutrients and exchangeable cations (Appendix A4).

A second trial was established on an 8-year-old agricultural fallow land in Dassari village (N 10°48'52.3" and E 1°7'53", altitude 196 m a.s.l), at 8-10 km from the experimental site in Pouri (Appendix A2). The field data collected from this trial were used to validate allometric equations (Noulèkoun et al. 2018a). The soil is a gleyic lixisol (hyperferritic), characterized by an overall high clay content (70.6 %) particularly increasing in the subsoil (Appendix A4). Compared to the Pouri site, the soil is deeper and less acidic (pH 5.9) with a higher water holding capacity but lower concentration of available phosphorus (P) (Appendix A4).

2.2 Tree species

Five (semi-) deciduous shrub and tree species were included in the experiment: *Moringa oleifera* Lam. (drumstick, small tree, Moringaceae), *Leucaena leucocephala* Lam. (leucaena, medium-sized tree, Fabaceae), *Jatropha curcas* L. (physic nut, shrub or small tree, Euphorbiaceae), *Anacardium occidentale* L. (cashew, medium-sized tree, Anacardiaceae) and *Parkia biglobosa* Jacq. (African locust bean, tree, Fabaceae). The species were selected based on reported information about their potential ability to grow on degraded lands and socio-economic importance for local communities (Noulèkoun et al. 2017a, 2018a).

Seedlings of the five species were raised in a tree nursery from seeds collected from mature trees growing in the study area (Noulèkoun et al. 2018a). The seedlings were grown in polyethylene tubes ($\phi=5$ cm, 15 cm long) filled with a substrate of local soil mixed with organic material. No fertilizer was applied to the seedlings in the nursery.

2.3 Experimental setup

The seedlings were planted in July 2014 on both sites at the age of 2.5-4 months. During planting, the substrate was left attached to the roots, but the polyethylene tube was removed. Prior to planting, the sites were ploughed, levelled, cleared of grasses and sparse woody debris and fenced to protect the seedlings. The seedlings were planted in manually dug pits with 30 cm radius and 15 cm depth and arranged in mono-species plots that were randomized.

Three experimental factors expected to influence the establishment and early growth of saplings were studied: (i) tree species (5), (ii) nutrient (1 level), and (iii) water availability (1 level) imposed through drip irrigation (Figure 1 in Noulèkoun et al. 2017b), and fertilization by manuring (Appendix A5). The study thus consisted of four treatments following an increasing gradient of resource availability: control (C, neither irrigation nor fertilization), fertilization (F), irrigation (I), and fertilization + irrigation (IF). The species and irrigation factors were arranged in a fully factorial design with three replications while manuring was introduced as a random nested factor (Appendix A6). The species were randomly distributed on 30 plots, each 12 m x 8 m (Appendix A7). Each plot

contained 48 seedlings at 2 m x 1 m spacing, resulting in an initial density of 5,000 saplings ha⁻¹ (Appendix A6). Manual weed control was performed when needed. Neither pesticides nor fungicides were applied in the course of the experiment.

Manure was applied during the rainy seasons at 2.5 and 11 months after planting (MaP), each time at the rate of 1 kg per plant (Figure 2 in Noulèkoun et al. 2017a). Manure applications supplied on average 18.7% carbon (C), 1.2% N, and 0.8% P to the saplings in the F and IF treatments. Supplemental irrigation was implemented during the dry season only via an adapted drip irrigation system consisting of perforated plastic bottles positioned ca. 15 cm next to each plant (Figure 1 in Noulèkoun et al. 2017b). Irrigation water was supplied at 0.5 L per sapling per day to meet 30% of the evaporative demand (ca. 6 mm day⁻¹). Therefore, trees in the I and IF treatments received in addition to 33 mm of rainfall, 105.5 mm of water during the dry season, while those in the C and F treatments only received water from rainfall. The same experimental layout was implemented on both sites, although the trial on the fallow land in Dassari included only two of the five species (i.e., *J. curcas* and *L. leucocephala*).

2.4 Field measurements and laboratory analyses

Tree survival, morphological traits (i.e., height (H), stem diameter (D), rooting depth (RD) and maximum extent of the lateral roots (RE)), aboveground biomass (AGB) and belowground biomass (BGB) were measured on 2-6 randomly selected saplings at 5 MaP (covering the 2014 rainy/growing season), 11 MaP (covering the 2014-2015 dry season) and 15 MaP (covering the 2015 rainy season).

Before transplanting the nursery-grown seedlings in the plots, 10 representative individuals of each species were randomly chosen from the overall stock to determine the mean reference values for all morphological traits and biomass components monitored during the study period (Table 1 in Noulèkoun et al. 2017a). Details on the subsequent field measurements and laboratory analyses are presented in Noulèkoun et al. (2017a, b, 2018a, b).

2.5 Modeling approach

The Water, Nutrient and Light Capture in Agroforestry Systems (WaNuLCAS) model (version 4.3) was used to reproduce the growth dynamics of saplings of two species (*J. curcas* and *M. oleifera*; Appendix A8). WaNuLCAS was developed by van Noordwijk and Lusiana (1999) to improve the understanding of tree–soil–crop interactions in agroforestry systems, with emphasis on above- and belowground interactions. The model simulates the daily tree growth as a function of water, nutrient and light availability at plot scale. The modeled plot is represented horizontally by four zones and vertically by four soil layers where trees can be positioned (Figure 2 in Noulèkoun et al. 2018b). Details on the input data for WaNuLCAS as well as the description of the uptake of above- and belowground resources by the plant as well as the water balance in WaNuLCAS are presented in Noulèkoun et al. (2018b).

The model was calibrated with the 2-year experimental data from the F treatment and validated with the data from the C, I and IF treatments. The validated model with the C treatment, which represents the common, low-input silvicultural practice in the study area, was used to perform 35 runs, each covering 2 consecutive years over the historical climate period of 36 years (1981-2016), to quantify the strength of relationships between annual AGB growth and climate indicators derived from the historical climate data (Table 3 in Noulèkoun et al. 2018b). Furthermore, two soil and rooting depth scenarios (either shallower [33.3 cm] or deeper [75 cm] than at the experimental site) were performed under two contrasting water stress conditions (severe and mild) to evaluate the effects of deep rooting in reducing sapling sensitivity to extreme climate events (Noulèkoun et al. 2018b).

2.6 Statistical and modeling analysis

The methods employed to analyze the growth performance and responses of the tree species to the silvicultural treatments over the 15-month study period are summarized in Table 2.1. Overall statistical analyses to detect significant differences in species responses to treatments involved the use of linear mixed-effects models and ANOVA. For all analyses, general tests of normality and homogeneity of variance were

conducted, and the robust standard error was used to control for any deviation from these assumptions in the data (Noulèkoun et al. 2017a, b, 2018a). A least significance difference (LSD) test was used to compare means when significant treatment effects were found. A significance level of $p < 0.05$ was used as the threshold value. The statistical software STATA 14 (StataCorp 2015) and R version 3.4.3 (R Core Team 2017) were used for the data analyses.

The performance of WaNuLCAS was evaluated using the goodness of fit (GOF) procedure suggested by Loague and Green (1991) along with the coefficient of determination (R^2). To assess the climate sensitivity of sapling growth, a generic approach was tried as an alternative to the traditional dendrochronological analysis (Noulèkoun et al. 2018b). The approach combined: (i) the simulation of the early growth (i.e., first two years after planting) of trees under historical climate (1981-2016) using WaNuLCAS, (ii) the identification of the most important climate indicators driving sapling AGB growth using linear mixed-effects models and climate sensitivity indices, and (iii) the quantification of the effects of year-to-year climate variability on sapling growth based on the climate indicators identified in (ii). The representativeness of the empirical climate data vis-à-vis the long-term climate variability was assessed using descriptive statistics (Table 3 in Noulèkoun et al. 2018b).

Table 2.1 Summary of data analysis methods

Research objective (section 1.4)	Goal	Method (source)
1	Assess the early establishment (survival) of the five MPTS	Kaplan-Meier survival analysis (Kaplan and Meier 1958)
1	Classification of the five MPTS into functional groups (fast- and slow-growing) and analysis of the plastic responses of the shoot- and root-level functional traits to treatments	Classical approach of growth analysis (Evans 1972)
2	Distinguish between ontogenetically modulated and treatment-induced shifts in biomass partitioning to belowground in the five MPTS	Clasmometric and allometric analysis (Poorter and Sack 2012; Poorter et al. 2015)
3	Establish empirical allometric relationships between plant biological traits (height, stem diameter and biomass of different tree fractions) for the five MPTS	Fitting non-linear regressions to equations derived from the conventional power-law equation (e.g., Baumert and Khamzina 2015)
4	Examine climate-growth relationships for two selected MPTS	Climate sensitivity analysis of the simulated early growth using climate sensitivity indices (Myers-Smith et al. 2015)
4	Reproduce the field-observed growth dynamics of two MPTS as well as simulate their early growth under historical climate conditions (1981-2016) and their adaptation strategy to drought	Process-based modeling and scenario analysis using WaNuLCAS (van Noordwijk et al. 1999)

3 RESULTS AND DISCUSSION

3.1 Sapling growth as impacted by functional group and resource availability

In this study, significant interactions between species and silvicultural treatments (i.e., fertilization and irrigation), as reflected in morphological traits and biomass allocation, showed that fast- and slow-growing species differed in their responsiveness to resource availability (Noulèkoun et al. 2017a, b). In particular, the fast-growing species (*J. curcas*, *L. leucocephala* and *M. oleifera*) were characterized by a more pronounced aboveground (i.e., H, D and AGB) development and a more vigorous response to increased resource availability during the two rainy seasons than the slow-growing species (*A. occidentale* and *P. biglobosa*), indicating their exploitative use of resources. In contrast, the slow growers depicted growth patterns associated with a more conservative use of resources, thus showing a higher plastic response to the treatments in both shoot and root morphological traits and a greater investment in belowground development (i.e., higher root to shoot ratio, RSR) during the dry season (Noulèkoun et al. 2017a, b, 2018a).

The comparison of intra-specific trait plasticity in response to resource availability and the range of treatment-induced increases in traits across treatments and assessment periods revealed an overall greater plastic response of the slow growers compared to the fast growers (Noulèkoun et al. 2017a, b). The relatively lower plasticity of fast-growing species than that of slow-growing species across soil resource gradients was also reported for seedlings of nine tropical tree species grown in a shadehouse pot experiment (Baraloto et al. 2006). While a combination of traits associated with a rapid resource acquisition permits a quick growth across a wide environmental gradient, the lower trait plasticity and the higher costs of 'fast' traits may compromise the potential growth, particularly in resource-poor environments (Baraloto et al. 2006; Reich 2014). Evidence from the presented studies (Noulèkoun et al. 2017a, b) about the performance of the fast-growing species during the dry season supports the concept of this trade-off between the rapid growth and resource availability. The slow-growing species in this afforestation experiment appeared to tolerate resource (i.e., nutrient and water)

deficiencies due to their conservative resource-use strategy (Noulèkoun et al. 2017 a, b).

Although the fast- and slow-growing species showed contrasting resource-use strategies, their adaptive responses to water and nutrient stress should accord with the optimal partitioning theory (OPT; Poorter and Sack 2012). That is, saplings would respond to low nutrient and water availability by allocating more carbohydrates to those organs which support the acquisition of these resources, i.e. the roots (Bloom et al. 1985). In agreement with the OPT, the analysis of morphological trait expression revealed that saplings exhibited longer lateral roots and deeper rooting depth in response to nutrient and water limitation, respectively (Noulèkoun et al. 2017a). In contrast, shifts in biomass allocation to belowground organs in response to nutrient and water limitations were not always consistent across treatments and species, and were mainly mediated by ontogeny. Consequently, patterns of biomass partitioning in the tested species, after controlling for ontogeny, provided little support to the OPT (Noulèkoun et al. 2017b). The generally modest manifestation of root-to-shoot biomass adjustment in response to low resource availability and subsequently poorer performance of saplings under water- and nutrient-stress conditions (i.e., control treatment) observed in this study were also reported for juvenile trees of loblolly pine and cottonwood genotypes in humid sub-tropical conditions (Coyle and Coleman 2005; Coyle et al. 2008). The evidence combined indicates the need for silvicultural interventions to support the establishment of multi-species tree plantations on degraded cropland.

3.2 Candidate tree species and silvicultural management for the afforestation of degraded cropland

The differential eco-physiological characteristics and responses of the tree species to management observed in the experiment suggest that the screening of potential candidates for the afforestation of degraded croplands should rely on a set of suitable indicators, including survival rate, growth potential and trait plasticity. These allow the appraisal of the species ability to establish on degraded cropland and tolerate the

prevailing environmental stressors. In this study, the fast-growing and drought-tolerant *J. curcas*, *L. leucocephala*. and *M. oleifera* showed lower mortality compared to the slow-growing, drought-sensitive *P. biglobosa* (Noulèkoun et al. 2017a). No mortality was recorded in *J. curcas* stands over the study period, confirming the common claim of its suitability for reclaiming degraded lands in dry areas (Achten et al. 2010). Most of the plant mortality peaks occurred due to water stress during the long dry season (Khurana and Singh 2001), and the supply of even modest amounts of water dramatically reduced the dry-season and post-planting mortality of *P. biglobosa* (Noulèkoun et al. 2017a). Extending the habitat range of drought-sensitive species to degraded croplands in dry areas may thus benefit from supplemental irrigation to curb the effect of drought stress on their establishment (Ibid).

Given the low inherent soil fertility and the semi-arid climate conditions of the study area, the supply of manure and water generally facilitated tree establishment and growth. The effect of fertilization on sapling growth was overall greater than that of irrigation and even than that of irrigation plus fertilization for some growth parameters, e.g., biomass production (Noulèkoun et al. 2017a, b), emphasizing the relatively greater importance of nutrient over water stress for sapling growth, which is common in semi-arid regions (e.g., Reubens et al. 2011). Moreover, the higher total shoot and root productivity of the afforestation site compared to that of a neighboring 10-year-old fallow (naturally revegetated by shrubs and grasses) was, next to the choice of plant species, also due to silvicultural management (Noulèkoun et al. 2017b). Overall, the observed increases in growth induced by fertilization and irrigation confirm the positive effects of 'intensive' silviculture in overcoming environmental constraints and increasing plantation productivity (Coyle and Coleman 2005; Coyle et al. 2016) on the degraded cropland.

Desirable characteristics of the fast-growing species, such as high survival and growth rates, biomass production potential and plastic responses to silvicultural treatments during the rainy seasons make them most attractive candidates for afforestation and certainly when farmers can afford to supply nutrients and water to the saplings (Noulèkoun et al. 2017a, b). The slow-growing species, characterized by a slow

initial growth, which is often associated with a long lifespan (Larcher 1995), maintained growth under resource-poor conditions during the dry season (Noulèkoun et al. 2017a). Although the slow-growing species did not develop as quickly as the fast growers, their ability to adjust to stress factors would allow for extending afforestation practice to a broader range of degraded lands (Aubrey et al. 2012; Noulèkoun et al. 2017a, b). A multi-species afforestation system, combining fast- and slow-growing species, may therefore help to reduce investment risks and increase the benefits of tree plantations for smallholder farmers (Noulèkoun et al. 2017a, b).

3.3 Climate change impacts on sapling growth

Besides soil water and nutrient limitations on degraded cropland, climate change and variability represents another influential factor for the success of afforestation. Uncertainty surrounding climate projections challenges assessments of future impacts of climate change on tree growth and the management decisions for forests and tree plantations (Spittlehouse and Stewart 2003; Millar et al. 2007). Given that past climatic variability has led to different physiological adaptations and growth strategies of species (e.g., Cook et al. 2001; Teets et al. 2018), it is postulated that the effects of future climatic changes on tree growth could be predicted from the analysis of species-specific responses to past climate conditions (Friedrichs et al. 2009). The analysis of climate sensitivity of two afforestation species (*J. curcas* and *M. oleifera*), focusing on crucial early development stages, revealed that water deficits induced by drought (indicated by annual water deficit [AWD]) and dry spells (indicated by the length of the longest dry spell [LDSP]) were the main factors likely to jeopardize the success of afforestation under the semi-arid climate conditions of Benin (Noulèkoun et al. 2018b). These water-related indicators were likewise reported as the most important climate variables influencing the growth of tropical tree species (e.g., Castro et al. 2015; Comita and Engelbrecht 2014).

Moreover, climate sensitivity of sapling growth to drought and the climatic drivers with the largest explanatory power (i.e., AWD, LDSP and length of dry season [LDS]) differed between year 1 and year 2 since tree planting for both species

(Noulèkoun et al. 2018b). For instance, biomass growth was more sensitive to the temporal distribution of rainfall (LDSP) in year 1, whereas variables related to the amount of rainfall (AWD and LDS) were most influential on growth in year 2. Increasing variability in rainfall distribution and the resulting effects on forest and plantation productivity has received less attention in published research than the impacts of shifts in the mean precipitation regimes (e.g., Wullschleger and Hanson 2003). The current results demonstrate that rainfall variability expressed here by LDSP significantly limits growth, particularly at the earliest stage (year 1) when the tree root systems only start to develop. The impacts of reduced rainfall amounts on early growth were evidenced by a reduction in AGB growth of 14-31% (Noulèkoun et al. 2018b). These findings suggest that the increase in water stress and the number of consecutive dry days projected for northern Benin through continued warming (MEHU 2011; Sylla et al. 2016a) may impose additional constraints to afforestation efforts in the future, because of the adverse impact on early plant growth.

Nevertheless, scenario analysis with the WaNuLCAS model showed that increased rooting depth might be an effective adaptation to the future climate constraints. In particular, the simulation results indicate that deep-rooted saplings performed better in both extreme wet and dry conditions, and were less sensitive to drought than their shallow-rooted counterparts (Noulèkoun et al. 2018b). This is possibly caused by the ability of deep-rooted saplings to exploit soil water available in deeper horizons, which in turn allows continued photosynthetic activity even during drought (e.g., Hartl-Meier et al. 2014).

Given that the weather data of the experimental years (2014 and 2015) represented one or a few of the many possible weather sequences for the study site, their representativeness vis-à-vis the long-term (1981-2016) climate variability was evaluated based on the most important climate indicators (AWD, LDSP, LDS and the annual total wet-day precipitation [ATWP]). The results show that the experimental years, particularly the year 2015, were characterized by extreme drought conditions and less rainfall (Table 3 in Noulèkoun et al. 2018b). The observed patterns are in line with climate change projections for West Africa (Sylla et al. 2015, 2016a). The performance

of the saplings during the two years is therefore a conservative estimate of what can be expected in years closer to the current average values, and is more representative of the expected tree growth under projected climate conditions (Noulèkoun et al. 2018b).

3.4 Methodological considerations

3.4.1 Allometric approach for estimating tree biomass

The field-based results of the afforestation experiment permitted the estimation of sapling above- and belowground biomass accumulation for each afforestation species based on empirical relationships with easily measured dimensions of the plant stem. The results reveal that the power law model using basal diameter (D) as the single predictor, commonly reported as the ideal of tree allometry in many studies (e.g. Baumert and Khamzina 2015; Kuyah et al. 2012, 2016), was not automatically appropriate for all species tested (Noulèkoun et al. 2018a). For example, the power model with D and H as independent variables best predicted AGB and BGB for the slow-growing species *P. biglobosa*. Moreover, the incorporation of the scaling coefficient (*c*) of the H–D relationships into the allometric equations showed that this coefficient could be considered as a proxy for predicting biomass based on D for broader environmental gradients for one of the species (*J. curcas*). This obviates the need for destructive sampling and offers a good trade-off between accuracy, cost and practicability at both local and landscape levels (Brown et al. 1989; Kuyah et al. 2012; Noulèkoun et al. 2018a).

Regression diagnostics indicated that besides R^2 , model performance statistics such as the mean absolute percentage error (MAPE) and the mean relative error (MRE) should be considered when assessing allometric model fitness, because high R^2 values alone do not necessarily guarantee precise estimates (Sileshi 2014; Baumert and Khamzina 2015). Furthermore, the predictive power of the equations developed was influenced by the plant deciduousness, suggesting that more accurate AGB predictions for drought-deciduous species can be obtained with equations based on woody fractions (Baumert and Khamzina 2015; Noulèkoun et al. 2018a).

However, applying the empirical data in published allometric equations for *J. curcas* resulted in substantial prediction errors (MRE up to 134%), emphasizing that

caution must be taken when applying allometric functions to data beyond the initial calibration ranges (Rothman 2002; Kuyah et al. 2012; Sileshi 2014; Noulèkoun et al. 2018a). The use of the generalized allometric equation developed by Brown (1997) for dry forests, commonly applied to estimate biomass in tropical forests for carbon accounting, led to a substantial overestimation ($404\% < \text{MRE} < 1235\%$). In contrast, the use of globally derived RSR (e.g., IPCC default RSR) to estimate sapling BGB will result in underestimations (Noulèkoun et al. 2018a). These findings altogether emphasize that accurate quantification of the carbon sequestration potential of young plantations will require site-specific and locally derived allometric models and a RSR representative of the plant population under study (Ibid).

3.4.2 Process-based modelling of tree growth dynamics and climate sensitivity

The process-based modeling approach integrated the allometric equations with further parameters relevant for plant-soil-atmosphere relationships and enabled the simulation of tree growth in a young plantation system. The analysis of the model performance based on the GOF statistics indicated the model's ability to simulate accurately the H, D and AGB under various silvicultural management options (Noulèkoun et al. 2018b). However, the model overestimated D and AGB during the dry season due to its limited capacity to account for drought-induced trunk shrinkage and litterfall. The simulation of D and AGB is strongly influenced by litterfall in WaNuLCAS. Thus, the lack of field-observed litterfall data for the drought-deciduous species might explain the poor prediction of these parameters during the dry season (Walker et al. 2007). An accurate calibration of the litterfall, however, requires data collected over a large range of environmental gradients and from tree species of different ages (Noulèkoun et al. 2018b).

The integration of multi-source data in the common modeling framework enlarged the scope of tree growth analysis beyond the specific settings of the experimental site. In particular, after integrating historical climate data and calculated climate sensitivity indices, the scenario-based modelling analysis allowed for predictions of potential growth trajectories and tree root adaptation in response to changing

climate (Noulèkoun et al. 2018b). This generic approach for assessing climate sensitivity of trees presents a distinct advantage over the classic dendrochronology because it uses the actual biomass increment rather than tree-ring widths or biomass increments derived from tree rings (Bouriaud et al. 2005; Foster et al. 2014), thereby avoiding challenges associated with missing tree rings in young trees or other problematic features of wood anatomy in tropical trees (Brienen and Zuidema, 2006; Herrera-Ramirez et al. 2017).

However, WaNuLCAS does not yet include a direct representation of the effect of temperature and CO₂ on plant growth, nor does it account for physiological processes associated with water stress such as cell damage (Walker et al. 2007; van Noordwijk et al. 2011). Adding these features would allow the simulation of the effects of increased temperature and/or CO₂ on tree growth and further assessment of future climate change effects, particularly important in drought-prone environments. Coupled with long-term field data, this would increase confidence in the validity of the model outputs and extend its range of applicability beyond limits recognised thus far.

In combination, field experiments and models can provide for more robust results than experiments alone would do. However, models even with relatively modest data requirements have to be supplied with extensive empirical data. To reap the potential benefits from such a combination of complementary approaches, field experiments need to be carefully planned, designed and monitored in accordance with the demands of the model envisaged, and aim to add to and enhance the model's capabilities further.

4 CONCLUSIONS AND OUTLOOK

4.1 Conclusions

Re- and afforestation has been globally promoted over the last decades as a way to revive degraded lands, achieve land degradation neutrality and improve livelihoods. However, it often proceeds based on general recommendations not tailored to the site-specific conditions of degraded lands, which explains the common failures of these efforts. Therefore, there is need for a comprehensive evaluation of the growth dynamics and performance of tree species considered in afforestation under the environmental conditions prevalent on degraded lands using both experimental and simulation tools to support the increasing afforestation projects.

This study contributes to such an evaluation for the SSZ of northern Benin by enhancing knowledge on the eco-physiological processes mediating the early growth dynamics of five tree species and identifying appropriate silvicultural practices for the management of young plantations. The following main conclusions can be drawn:

- The mixed cultivation of fast- and slow-growing species is most promising for reducing the risk of failure and enhancing the overall benefits from afforestation of degraded croplands.
- Overall, the supply of the growth-limiting resources, i.e. water and nutrients, resulted in increased survival rates and positive growth responses in the tested species. Silvicultural management such as application of organic fertilizer and deficit irrigation will thus benefit current and future afforestation activities.
- Sapling aboveground biomass growth responded strongly to annual water deficit, length of the longest dry spell and length of dry season suggesting that water availability will likely play an increasingly important role in limiting future sapling growth. Deep rooting reduced the sensitivity of sapling growth to extreme drought, indicating the advantage of tree genotypes with deep root systems in the face of global warming.
- Process-based modeling allowed capitalizing on experimental field data through their integration and synthesis, and can be used to broaden the scope of site-

and time-specific analysis of growth responses of trees to changing environmental conditions, thus entailing significant promise for sustainable afforestation planning.

- The combination of experiments and modeling provided a valid novel approach particularly for assessing the impacts of climate change on the early growth of afforestation species, and should be further developed for other relevant applications.

4.2 Outlook

The choice of suitable tree species for the afforestation of degraded croplands based solely on the assessment of early growth dynamics of tree species may raise concerns about their long-term growth potential. Although the importance of the relative growth rate as an effective early indicator of long-term growth potential of woody species suggested that the current findings can be regarded as a proxy of further growth (Noulèkoun et al. 2017a), studies covering later growth stages should quantify the long-term productivity and stress tolerance of forest plantations on degraded croplands. Silvicultural management such as thinning and pruning would also need to be explored and adjusted to the changing needs of tree plantations, particularly when aiming to integrate intercropping with annual crops in the longer run. Given the substantial biomass and carbon stock in the 15-month-old afforestation system, particularly in the N₂-fixing *L. leucocephala* plots (Noulèkoun et al. 2017b, 2018a), the economic valuation of the growing goods and ecosystem services, such as carbon sequestration and biological N fixation, might reveal attractive co-benefits of afforestation (e.g., Djanibekov and Khamzina 2016; Baumert et al. 2018).

As global efforts on the re- and afforestation of degraded lands are rapidly increasing, there is a need to emphasize inclusivity of local communities and social acceptance of these land-use options. Currently, farmers in Benin hardly apply silvicultural measures to trees believing that they would grow without additional inputs after planting (personal communication with local farmers). Therefore, the cultivation techniques tested in this study have to be translated into guidelines for their

communication to foresters and smallholder farmers through agricultural extension services. Further socio-economic assessments would identify the conditions and possible policy incentives for local farmers to adopt the afforestation and silvicultural practices.

The aforementioned suggestions for follow-up research indicate the need for the study of structure and function of afforestation systems taking the whole agricultural land use mosaic and landscape connectivity into consideration. Different scientific disciplines should therefore come together in addressing various aspects related to the rehabilitation of degraded agricultural lands and sustainable land management in conjunction with development researchers, land-use managers, local communities and policy makers in both an inter- and transdisciplinary manner.

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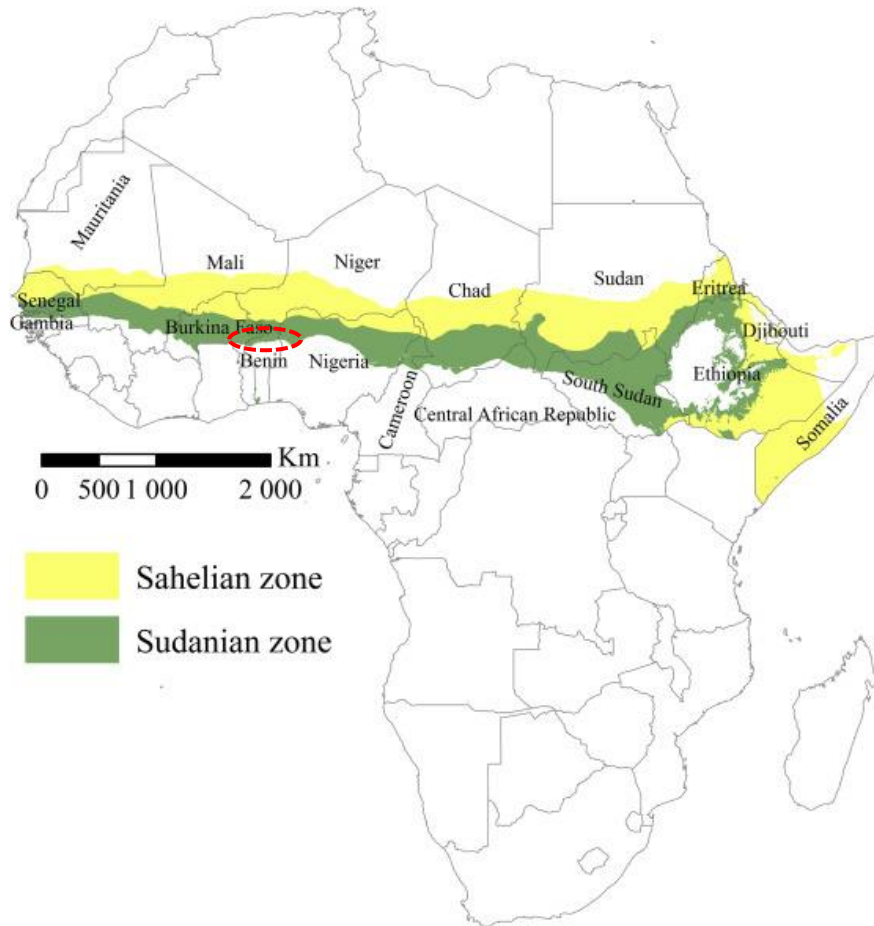
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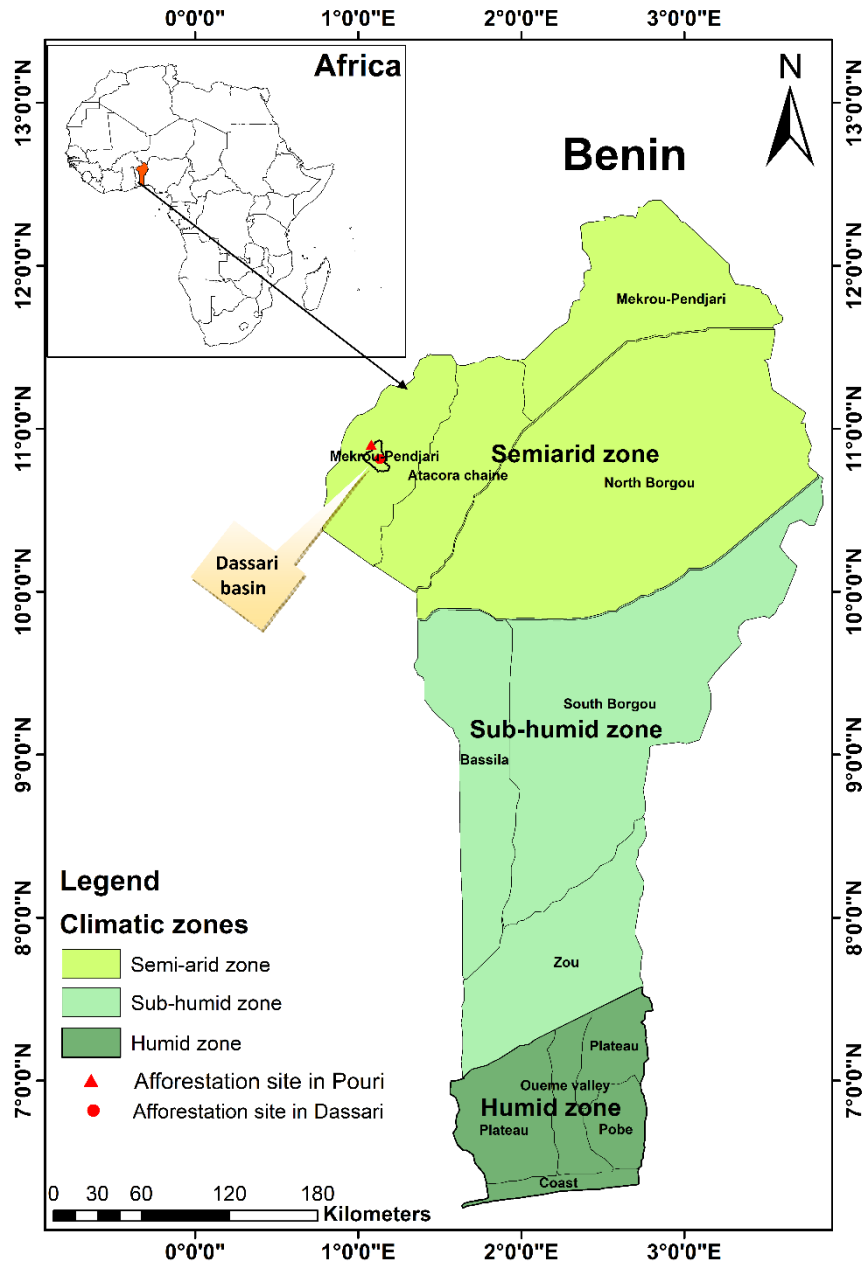
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6 APPENDICES

Appendix A1: Map of Sudano-Sahelian zone (SSZ) in West Africa. Source: Karlson and Ostwald 2016. Red marking: study location in northern Benin



Appendix A2: Location of afforestation sites in the semi-arid climate zone of north-western Benin



Appendix A3: Afforestation site at Pouri village at the onset of the experiment in June 2014 showing a cropland devoid of tree cover



Appendix A4: Soil physical and chemical properties at Pouri and Dassari afforestation sites at the onset of the experiment in June 2014

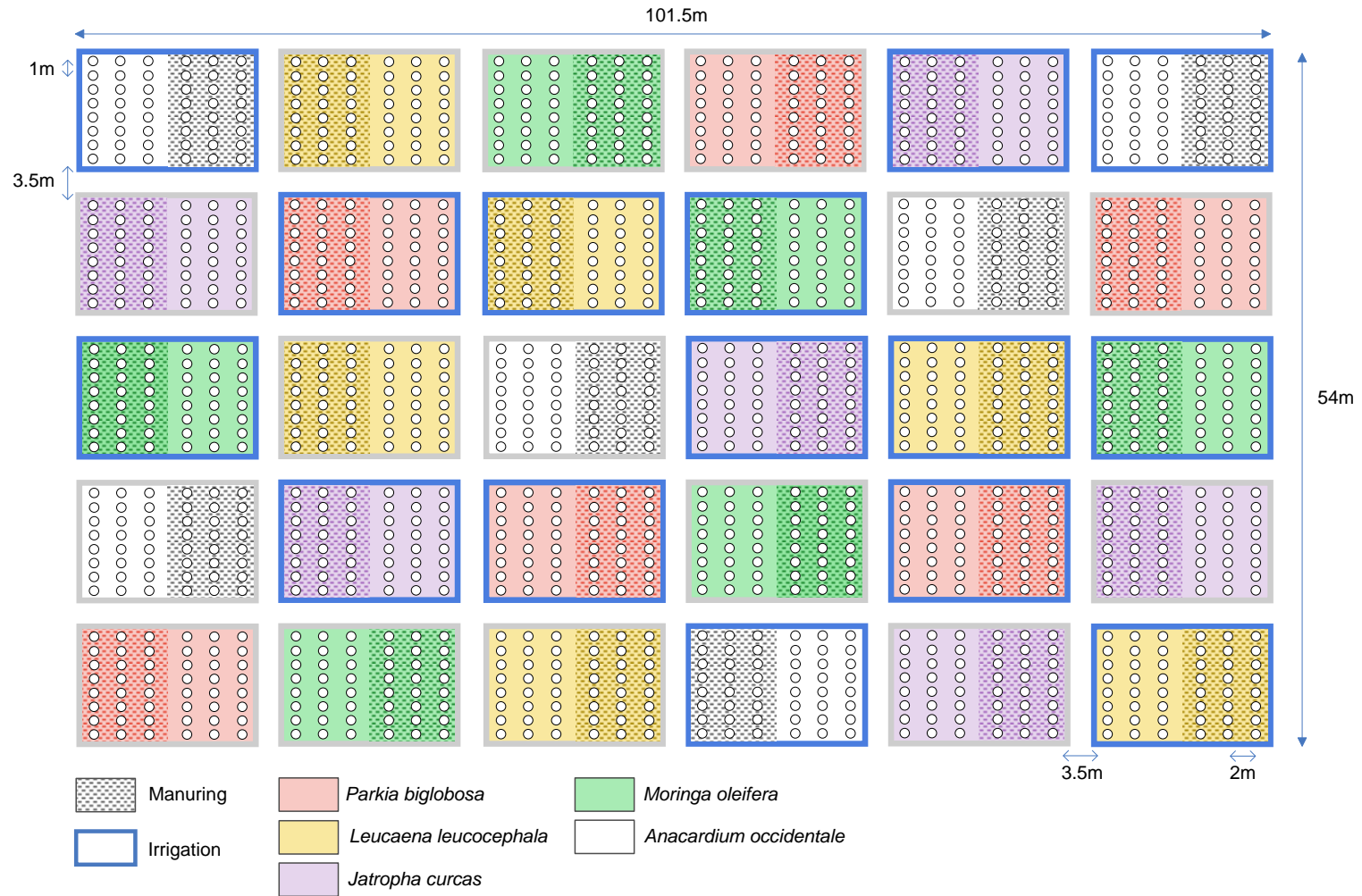
Parameter	Unit	Soil layer (cm)						
		Pouri				Dassari		
		0-5	16-29	16-30	30-50	0-14	14-55	55-128
Clay	(%)	11.8	15.7	25.5	29.4	19.6	31.4	70.6
Silt	(%)	31.4	35.3	33.3	37.3	31.4	27.5	9.8
Sand	(%)	56.9	49	41.2	33.3	49	41.2	19.6
BD	(g cm ⁻³)	1.5	1.5	1.6	1.6	1.5	1.6	1.8
pF 2.5	(% vol)	7.8	10.9	13.4	15.9	10.4	10.9	12.6
pF 4.2	(% vol)	3.8	5.3	4.5	4.8	4.7	5.4	6.0
OM	(%)	1.2	1.1	1.0	1.0	1.9	1.1	1.0
C	(%)	0.7	0.6	0.6	0.6	1.1	0.6	0.6
N	(%)	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Pav	(mg kg ⁻¹)	15.7	15.3	14.5	14.8	7.5	4.2	4.5
Kav	(mg kg ⁻¹)	90.7	77.6	16.1	20.2	32.2	14.1	20.2
CEC	(cmol kg ⁻¹)	4.7	6.0	5.2	5.3	8.5	8.0	6.3
pH-H₂O		5.3	5.2	5.7	5.8	5.8	5.9	5.9

Legend: BD: bulk density; pF2.5: field capacity; pF4.2: permanent wilting point; Ksat: saturated hydraulic conductivity; OM: organic matter; C: carbon; N: nitrogen; Pav: available phosphorus; Kav: available potassium; CEC: Cation Exchange Capacity

Appendix A5: First application of organic manure into the palnting hole around the stem base 2.5 months after planting



Appendix A6: Experimental layout of afforestation site at Pouri village



Appendix A7: Aerial image showing the 30 plots in the experimental site in Pouri village, north-western Benin



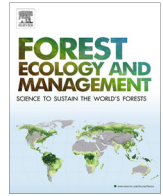
Source: Google Earth Imagery (2018)

Appendix A8: Afforestation site at Pouri village 15 months after planting, showing sapling of tree species *Moringa oleifera* (top) and *Jatropha curcas* (bottom)



Appendix B: The scientific articles (Noulèkoun et al. 2017a, b, 2018a, b) in their published form along with their related supplementary materials:

1. Noulèkoun F, Lamers JPA, Naab J, Khamzina A (2017a) Shoot and root responses of woody species to silvicultural management for afforestation of degraded croplands in the Sudano-Sahelian zone of Benin. *Forest Ecology and Management* 385:254–263. doi.org/10.1016/j.foreco.2016.11.018
2. Noulèkoun F, Khamzina A, Naab J, Lamers JPA (2017b) Biomass allocation in five semi-arid afforestation species is driven mainly by ontogeny rather than resource availability. *Annals of Forest Science* 74:78. [doi:10.1007/s13595-017-0676-4](https://doi.org/10.1007/s13595-017-0676-4)
3. Noulèkoun F, Naab J, Lamers JPA, Baumert S, Khamzina A (2018a) Sapling biomass allometry and carbon content in five afforestation species on marginal farmland in semi-arid Benin. *New Forests* 49(3):363-382. doi.org/10.1007/s11056-017-9624-2
4. Noulèkoun F, Khamzina A, Naab J, Khasanah N, van Noordwijk M, Lamers JPA (2018b) Climate change sensitivity of multi-species afforestation in semi-arid Benin. *Sustainability* 10(6):1-23. [doi:10.3390/su10061931](https://doi.org/10.3390/su10061931)



Shoot and root responses of woody species to silvicultural management for afforestation of degraded croplands in the Sudano-Sahelian zone of Benin



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West Africa

ABSTRACT

In the Sudano-Sahelian zone of West Africa, where deforestation and cropland soil degradation occur at alarming rates, the (re-)introduction of trees on degraded lands can improve and sustain farming systems and landscapes. The shoot and root morphological traits of five woody species introduced to degraded cropland were assessed with a particular focus on the survival, early establishment and growth of saplings subjected to manuring (1 kg per plant) and drip irrigation (0.5 L of water per plant per day). Functional traits of the woody above- and belowground organs of field-grown plants were monitored for the first 15 months after planting, covering two growing (rainy) seasons and one dry season. The high survival rate (>60%), combined with a very low incidence rate (<1%), for all species was evidence of successful establishment overall. The highest survival rates (94–100%) were observed in *Jatropha curcas* L., *Leucaena leucocephala* Lam. and *Moringa oleifera* Lam. The mortality rate of the most drought-sensitive species *Parkia biglobosa* Jacq. could be reduced ten-fold through supplemental irrigation during the dry season. The fast-growing *L. leucocephala*, *M. oleifera* and *J. curcas* had higher values for shoot-level traits than did the slow-growing *Anacardium occidentale* L. and *P. biglobosa*. Fertilization and irrigation enhanced the shoot growth of both the fast and slow growers during the dry and growing seasons. In contrast, belowground development was either increased or reduced by fertilization and irrigation during the growing and dry seasons, but the slow growers demonstrated a more plastic response to these treatments than did the fast growers. Among the studied traits, the relative growth rate of plant as a whole (i.e. shoots and roots combined) exhibited the greatest plastic response to resource availability, thus suggesting its application in screening candidate species for afforestation efforts. Overall, the five studied species were considered suitable for the afforestation of degraded croplands, while the early growth and establishment of saplings could be boosted by irrigation and a supply of manure.

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1. Introduction

With increasing severity and to an increasing extent, cropland degradation in sub-Saharan Africa has become a major threat to food security, environmental health, and human well-being, particularly in the drylands (Adams and Eswaran, 2000; Eswaran et al., 2001; Bai et al., 2008). To counterbalance this and ease growing food deficits, the farming population is forced to place more pressure on existing land resources, including marginal croplands that are ill-suited for agriculture, thus accelerating environmental

degradation and lowering agroecosystem productivity (Vlek et al., 2008).

Reforestation, afforestation, and tree-based farming with multi-purpose tree species have been recognized worldwide as a means to reverse land degradation and sustain agricultural systems (Chamshama and Nduwayezu, 2002; Garrity et al., 2010; Khamzina et al., 2012). For instance, *Jatropha curcas* L., a biofuel crop, has been extensively propagated to reclaim wastelands and restore soil productivity on marginal lands in the semi-arid tropics, although with variable success (Francis et al., 2005; Reubens et al., 2011; Baumert and Khamzina, 2015). The cultivation of nitrogen-fixing tree species, such as *Faidherbia albida* Del. and *Leucaena leucocephala* Lam., has been widely promoted to replenish soil nitrogen and alleviate fodder deficits (Orwa et al., 2009; Garrity

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et al., 2010; SPORE, 2015; Noulèkoun et al., 2016). Species with a high commercial value, such as *Moringa oleifera* Lam., *Anacardium occidentale* L. and *Parkia biglobosa* Jacq., have been advocated for use in afforestation (Edinger and Kaul, 2003), but empirical studies on their viability on degraded lands remain scarce.

Practical recommendations regarding the choice of tree species capable of productive growth on degraded croplands, which are characterized by water and nutrient limitations, may be more reliable with a better understanding of the functional traits, resource use strategies, and phenotypic plasticity of candidate tree species. Reich (2014) postulated the coordination of plant growth traits and resource use; rapidly acquiring a given resource at any organ level requires the same for other resources at the same organ level. This coordinated trade-off between functional traits and resource use results in fast- and slow-growing plants (Reich, 2014). The fast growers are exploitative resource competitors and show a more plastic response to increased resource availability than do slow growers. In contrast, slow growers pursue a more conservative resource use strategy, which allows them to maintain growth under resource-poor conditions (Reich et al., 2003b; Reich, 2014). Therefore, understanding the response of plants to the supply of resources involves a consideration of the ‘fast-slow’ plant economics spectrum which in turn will support the assessment of site-specific silvicultural practices aimed at the establishment of tree plantations on unproductive cropland (Aerts et al., 2007; Khamzina et al., 2008; Reubens et al., 2009).

When analyzing plant functional traits to understand the differences in growth responses to resource gradients (Chapin et al., 1993; Barbosa et al., 2014), rather than focusing on aboveground traits only, a whole-plant perspective is needed because responses might differ above- and belowground (e.g. Khamzina et al., 2016). For instance, variations in aboveground morphological traits related to leaves or shoots are primarily a response to differences in light interception and the assimilation of carbon, whereas morphological changes in the roots are usually responses to water and nutrient availability (Funk et al., 2007; Valladares and Niinemets, 2008; Coyle et al., 2016). The extent and pattern of changes in functional traits in response to resource availability (e.g., water, nutrients, and light) are commonly assumed to accord with the functional equilibrium theory, which assumes that plants allocate relatively more resources to organs that aid in the acquisition of the most limiting resource (Brouwer, 1963; Poorter et al., 2012). Because the evidence for this growth theory predominantly stems from (very) short-term studies, usually conducted in greenhouses and under artificial conditions to reduce complexity (Shipley, 2000), it is questionable whether these findings apply to woody species over time and in the field (Sack and Grubb, 2001).

Given the inherent risks for smallholder farmers on sub-Saharan African drylands who invest in afforestation, we examined the functional traits of multi-purpose tree species for which there had been little or mixed empirical evidence to date regarding their suitability for planting on degraded lands. Thus, in analyzing the shoot- and root-level morphological traits of five candidate species on degraded cropland in the Sudano-Sahelian zone of West Africa, we aimed to (i) assess plant establishment and growth characteristics on nutrient-poor and water-limited soil, (ii) identify and explain species-specific responses to silvicultural management practices, including supplemental irrigation and manuring during the growing and dry seasons, and (iii) identify species functional traits that may serve as a proxy for longer-term growth trends. On this basis, we identified those tree species and silvicultural management approaches that were most appropriate for use in the afforestation of degraded croplands.

2. Materials and methods

2.1. Study site

The arid Atacora department in northern Benin (Fig. 1) was selected as the study site because this region has been significantly affected by land degradation driven by deforestation and soil nutrient mining (Adegbedi et al., 1999; Mulder, 2000), threatening the sustainability of farming systems and exacerbating rural poverty (Saidou et al., 2003).

The climate in this region is semi-arid, characterized by one distinct rainy season (May to September) with a long-term average annual rainfall of 987 mm (for 1970–2010) followed by a prolonged dry season (September–May). Over the 15-month observation period, the annual rainfall was 757 mm in 2014 and 833 mm in 2015, below the long-term annual mean (Fig. 2).

The field experiment was carried out in Pouri village (N 10°54′8.4″ and E 1°44′7.4″; altitude 186 m.a.s.l) in Atacora (Fig. 1), which was selected following a four week-reconnaissance survey involving local and international forestry experts and Pouri community members. The selection criteria included (i) cropland impoverishment (judged by low nutrient stocks and crop yields), (ii) homogeneity in site conditions, (iii) site accessibility for regular measurements, and (iv) willingness of land owners to participate in the experiment and allocate croplands for afforestation. The area was savanna forest prior to being clear cut and then cropped with a successional three-year intercrop of either sorghum and cowpea or maize followed by yam for about a decade. Inorganic fertilizer was applied only during the maize-cowpea intercropping period.

The experiment was conducted on epipetric plinthosol (WRB, 2006) typified by a sandy-loam texture in the topsoil and clayey-loam in deeper profiles. The soil was limited to a depth of 50 cm by lateritic concretion and characterized by low water holding capacity, a low concentration of NPK, low cation exchange capacity (CEC), and relatively high acidity (Supporting Information Table S1).

2.2. Tree species and experimental design

Five woody species (Table 1) were selected due to their reported stress tolerance and socio-economic importance for the communities, as determined by a search of the literature, focus group discussions in the community, and an inventory of dominant tree species in the study region. All species are deciduous or semi-deciduous and have a habitat range within (sub) tropical climatic zones (Table 1).

Planting material for the woody species was obtained from a forest nursery near the experimental site where seedlings were grown in polyethylene tubes (ø 5 cm, 15 cm deep) filled with a substrate of local soil mixed with organic material. The seedlings were not fertilized. In July 2014, tree seedlings with an age of 2.5–4 months, were transplanted from the nursery to the experimental plots. During planting, the polyethylene tube was removed, but the substrate left attached to the roots.

Prior to planting, the site was cleared of sparse woody vegetation, ploughed, levelled, and fenced. The experiment compared a control treatment (with neither irrigation nor fertilization) with tree species performance under irrigation and fertilization. The species and irrigation treatments were arranged according to a fully factorial design with three repetitions whilst the manure application was introduced as a nested factor. The trial thus had a total of 30 plots (including the control plots) of 12 × 8 m², each containing 48 seedlings at a 2 m × 1 m spacing. The stand density at planting was thus 5000 trees ha⁻¹.

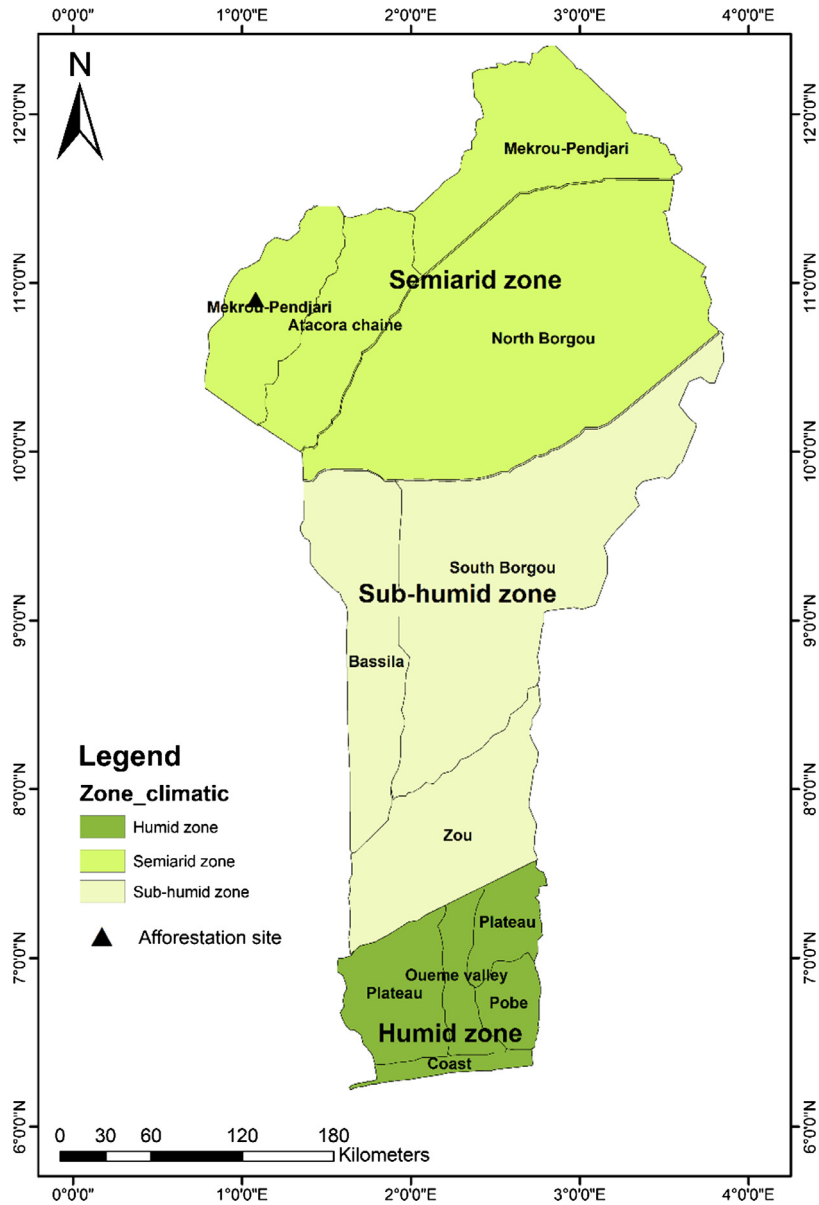


Fig. 1. Map of the climate zones and phyto-geographical districts of Benin showing the location of the afforestation site in Atacora department.

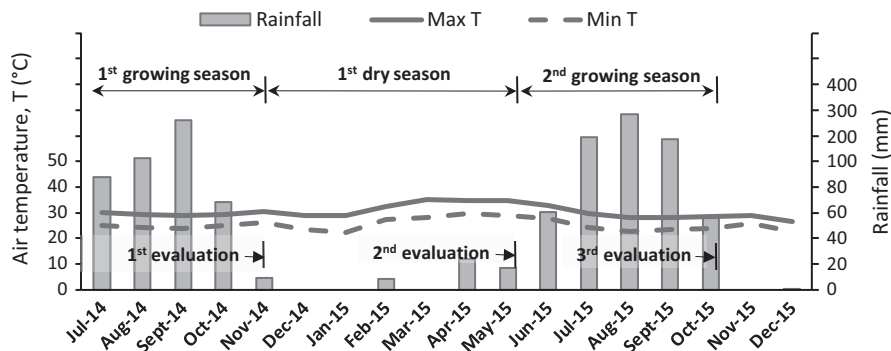


Fig. 2. Minimum and maximum ambient temperatures and seasonal rainfall during the study period (July 2014–December 2015) and indicated timings of plant trait evaluation.

Table 1

Characteristics of the tree species included in the afforestation trial and plant size ($n = 10$ for each species) at the onset of the experimentation (MaP = 0) in July 2014. The drought tolerance ranking is based on an agroforestry database (Orwa et al., 2009). Inherent growth rate ranking is based on the Useful Tropical Plants Database (Fern, 2014)¹, Edinger and Kaul (2003)² and Maes et al. (2009)².

Species	Family	Common name	Drought tolerance	Inherent growth rate	D	H	RD	RE
<i>Moringa oleifera</i> (Lam.)	Moringaceae	Drumstick tree	Tolerant	Fast ¹	0.54c	0.45a	0.12c	0.05a
<i>Jatropha curcas</i> (L.)	Euphorbiaceae	Physic nut	Very tolerant	Fast ²	0.99a	0.39a	0.12c	0.06a
<i>Leucaena leucocephala</i> (Lam.)	Fabaceae	Leucaena	Tolerant	Fast ¹	0.38d	0.30b	0.17a	0.06a
<i>Anacardium occidentale</i> (L.)	Anacardiaceae	Cashew	Tolerant	Slow ¹	0.78b	0.41a	0.17a	0.07a
<i>Parkia biglobosa</i> (Jacq.)	Fabaceae	African locust bean	Intermediate	Medium ¹	0.45 cd	0.27b	0.13b	0.08a

D: basal diameter (cm); H: height (m); RD: root depth (m); RE: maximum extent of lateral roots (m).

One-way ANOVA was used to identify trait differences between the tree species.

Means with a different letter within a column are significantly different at $p < 0.05$ according to the LSD post hoc test.

Supplemental irrigation was implemented during the dry season only using an adapted drip irrigation system consisting of perforated plastic bottles positioned ca. 15 cm next to each plant (Noulèkoun, 2017, in preparation). The saplings were irrigated at a rate satisfying 30% of the evaporative demand (equal to 0.5 L of water per sapling per day). In total, the saplings received 105.5 mm during the dry season (November 2014–May 2015), including 5 rainfall events amounting to 33 mm. Water was not supplied after the dry season to allow the post-irrigation effects on plants to be evaluated.

Fertilizer (manure) was applied 2.5 and 11 months after planting (MaP), each time at a weight of 1 kg per plant. A hole of 20 × 20 cm and 10 cm deep was dug around the plants and filled with manure. The manure contained on average 18.7% carbon, 1.2% nitrogen, and 0.8% phosphorus.

2.3. Monitoring plant survival and growth traits

Just before transplanting the seedlings from the nursery to the plots, ten representative seedlings of each species were randomly chosen to determine the mean reference values for all relevant morphological traits monitored during the study period (Table 1).

Seedling survival was assessed every fortnight by counting the number of living plants per plot. Dead plants were not replaced. At the beginning and end of the 2014 and 2015 growing seasons (i.e. 5, 11 and 15 MaP; Fig. 2), the height and diameter of 4–6 randomly selected trees per experimental plot were measured and consequently harvested. The entire root systems were excavated with hand tools. Border plants were excluded from this due to potential edge effects.

Tree height (H, m), i.e. the length of the highest shoot from the ground to the top was measured with a measuring tape. The diameter of the stem base (D, cm) was measured by taking the average of two diameter measurements (the longest and the shortest) using a digital calliper. When ramification had occurred at the stem base, the diameter was computed according to Baumert and Khamzina (2015):

$$D = \sqrt{\sum_{i=1}^n ((di)^2)} \quad (1)$$

where i represents the number of ramified stems measured at the stem base.

The maximum extent of the lateral roots (RE, m) was determined by measuring the length of the longest lateral root outward from the plant center using a measuring tape (Pérez-Harguindeguy et al., 2013). Rooting depth (RD, m) was measured following excavation. The foliage, shoots (stem and branches) and roots (coarse and fine fractions) were weighed separately with a portable scale and dried at 75 °C until they reached a constant weight. Consequently, the dry weights of all shoot and root fractions were deter-

Table 2

Variables used for the growth and morphological analyses.

Name of variable	Abbreviation	Unit
Relative growth rate in total biomass $(\ln(W_2) - \ln(W_1))/(T_2 - T_1)$	RGR _W	g g ⁻¹ month ⁻¹
Relative growth rate in diameter $(\ln(D_2) - \ln(D_1))/(T_2 - T_1)$	RGR _D	cm cm ⁻¹ month ⁻¹
Relative growth rate in height $(\ln(H_2) - \ln(H_1))/(T_2 - T_1)$	RGR _H	m m ⁻¹ month ⁻¹
Relative growth rate in rooting depth $(\ln(RD_2) - \ln(RD_1))/(T_2 - T_1)$	RGR _{RD}	m m ⁻¹ month ⁻¹
Relative growth rate in lateral root extension $(\ln(RE_2) - \ln(RE_1))/(T_2 - T_1)$	RGR _{RE}	m m ⁻¹ month ⁻¹

W: dry weight (g), D: basal diameter (cm); H: height (m); RD: root depth (m); RE: maximum extent of lateral roots (m), T: time (months). Subscripts refer to initial and final harvest.

mined and summed to obtain whole-plant biomass (W, g). Only woody above- and belowground fractions are reported in this study (Table 3) due to the focus on water and nutrient resource limitations and because we intended to identify indicators which can be more easily measured and understood by practitioners.

2.4. Data analyses

The classical approach involving harvest-interval calculations was used for the growth analyses (Evans, 1972). Due to the inherent bias in Grime and Hunt's (1975) equation for computing relative growth rate (RGR) based on the destructive harvest of several individuals, the relationship suggested by Hoffmann and Porter (2002) was used to estimate the RGR for the morphological traits (Table 2):

$$RGRx = \frac{\ln(X_2) - \ln(X_1)}{T_2 - T_1} \quad (2)$$

where RGR_x is the relative growth rate, X_1 and X_2 are the values of the measured trait at times T_1 and T_2 , and $\ln(X_2)$ and $\ln(X_1)$ are the means of the natural logarithm-transformed measured values at times T_1 and T_2 .

All statistical analyses were performed with STATA 14 (StataCorp., 2015). Kaplan-Meier survival analysis was used to estimate seedling survival curves (Kaplan and Meier, 1958). Through the log rank test, the equality of the survival functions between species was assessed. Harvested plants were considered missing values when estimating species-specific survival rates.

A linear mixed-effects model was used to assess differences in plant growth performance with respect to fertilization and supplemental irrigation, as well as their interaction. Because irrigation was applied during the dry season only, a separate model was used

Table 3
Significance levels ($P < 0.05$) of shoot (D, H, RGR_D, RGR_H) and root (RD, RE, RGR_{RD}, RGR_{RE}) traits by species, fertilization, irrigation, and their interaction effects for three assessment periods over the first 15 months after tree planting (MaP).

	Shoot-level traits											
	Basal diameter (D)			Height (H)			Relative growth rate in diameter (RGR _D)			Relative growth rate in height (RGR _H)		
	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP
Species	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Fertilization (manure)	<0.001	<0.05	<0.001	<0.01	n.s.	<0.001	<0.001	<0.001	<0.001	<0.01	<0.01	<0.001
Irrigation (drip)	n/a	n.s.	n.s.	n/a	n.s.	n/a	n/a	n.s.	n.s.	n/a	n.s.	<0.05
Species × fertilization	<0.05	<0.01	n.s.	n.s.	n.s.	n.s.	n.s.	<0.001	n.s.	n.s.	n.s.	<0.01
Species × irrigation	n/a	n.s.	<0.001	n/a	n.s.	<0.05	n/a	n.s.	<0.01	n/a	<0.01	<0.01
Species × fertilization × irrigation	n/a	<0.01	n.s.	n/a	<0.05	n.s.	n/a	<0.001	n.s.	n/a	<0.05	<0.001
Time			<0.001			<0.001			<0.001			<0.001
Time × species			<0.001			<0.001			<0.001			<0.001
Time × fertilization			<0.001			<0.05			<0.001			<0.01
Time × irrigation			n.s.			n.s.			n.s.			n.s.
	Root-level traits											
	Rooting depth (RD)			Maximum extent of lateral roots (RE)			Relative growth rate in rooting depth (RGR _{RD})			Relative growth rate in lateral root extension (RGR _{RE})		
	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP
Species	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	n.s.	<0.001
Fertilization (manure)	n.s.	n.s.	n.s.	n.s.	<0.001	n.s.	n.s.	n.s.	n.s.	n.s.	<0.05	n.s.
Irrigation (drip)	n/a	<0.001	n.s.	n/a	n.s.	n.s.	n/a	<0.001	<0.01	n/a	n.s.	n.s.
Species × fertilization	n.s.	n.s.	n.s.	<0.001	<0.001	n.s.	n.s.	n.s.	n.s.	<0.001	<0.01	n.s.
Species × irrigation	n/a	n.s.	n.s.	n/a	n.s.	<0.01	n/a	n.s.	n.s.	n/a	n.s.	<0.001
Species × fertilization × irrigation	n/a	n.s.	n.s.	n/a	<0.001	<0.01	n/a	n.s.	n.s.	n/a	<0.01	<0.01
Time			<0.001			<0.001			<0.001			<0.001
Time × species			<0.001			<0.001			<0.001			<0.001
Time × fertilization			n.s.			<0.01			n.s.			n.s.
Time × irrigation			<0.01			n.s.			<0.05			n.s.

n.s. = not significant; n/a = not applicable.

5 MaP covers the first growing season; during the dry season (5–11 MaP) supplemental irrigation was applied; 11–15 MaP covers the second growing season.

for each of the three evaluation periods: 0–5 MaP, 5–11 MaP, and 11–15 MaP. The random terms in the model were plot identity and fertilization (nested within plots), whereas species, fertilization, and irrigation were the fixed terms. Furthermore, the mixed-model was run by adding time to the fixed factors to assess the trend in plant responses over the assessment period. To control for any deviation from the assumption of normality in the tested variables, the robust variance estimates (robust) and unstructured covariance options in STATA (StataCorp., 2015) were used in the mixed-model.

Because the seedlings differed in their initial age (MaP = 0), age at transplantation was introduced into the model as a covariate controlling for the possible effect of age differences on plant performance. The inclusion of initial age only had significant effects on tree height. Additional covariates (the initial values of D, H, RD and RE) were checked, but due to the lack of significance, they were omitted from the final model.

Differences in mean RGR between functional groups do not necessarily equate to simple and consistent differences in any single trait or set of traits (Reich et al., 2003a). Thus, to rank the studied species based on their growth rates, the RGR of whole-plant biomass (RGR_w) between the initial and final harvest was used instead of the RGR of D (RGR_D), H (RGR_H), RD (RGR_{RD}) and RE (RGR_{RE}). An ANOVA was run to test for equality in the means of RGR_w between species.

An ANOVA was also employed to evaluate differences in trait plasticity, quantified as the coefficient of variation (CV, calculated as the standard deviation over the mean) between treatments (fertilization and irrigation) and assessment periods (Siebenkäs et al., 2015), for morphological traits at the shoot- (D, H, RGR_D and RGR_H) and root- (RD, RE, RGR_{RD} and RGR_{RE}) level, as well as between species. Unless stated otherwise, the mean values presented are from the original data and expressed per tree. The estimated least significance difference (LSD) is reported in this study to facilitate multi-

ple comparisons of the means in which significant treatment effects at a 5% level of significance are identified.

3. Results

3.1. Plant survival

The survival curves significantly differed between the five species ($\chi^2(4) = 233.79$; $p < 0.001$). The overall incidence rate, which is the measure of the frequency with which mortality occurs in a given population and in a defined time period, was very low (0.7%, i.e. only seven dead plants would be expected in 1000 trees over 15-month period). Apart from *J. curcas*, which experienced no mortality over this period, the survival curves for all other species exhibited a decreasing trend over time (Fig. 3).

For the remaining four species, peaks in mortality were observed at 0.5, 6, and 7.5 MaP, with several moderate mortality peaks that were species-specific (Fig. 3). At 15 MaP, high overall survival rates were recorded for *L. leucocephala* (98%) and *M. oleifera* (94%), whereas *A. occidentale* had a moderate survival rate of 87%. The decline in survival over time was most pronounced in *P. biglobosa*, which had the lowest survival rate (67%) and several mortality peaks. Except for *M. oleifera*, no mortality was recorded during the second growing season. Supplemental irrigation significantly increased the survival of *P. biglobosa* saplings ($P = 0.014$, data not shown), for which the mortality rate at 11 MaP was ten times higher in non-watered plots.

3.2. Species performance

The RGR_w for the entire study period was significantly higher for *L. leucocephala*, *M. oleifera* and *J. curcas* compared to *A. occidentale* and *P. biglobosa* (Fig. 4). Of the three fast-growing

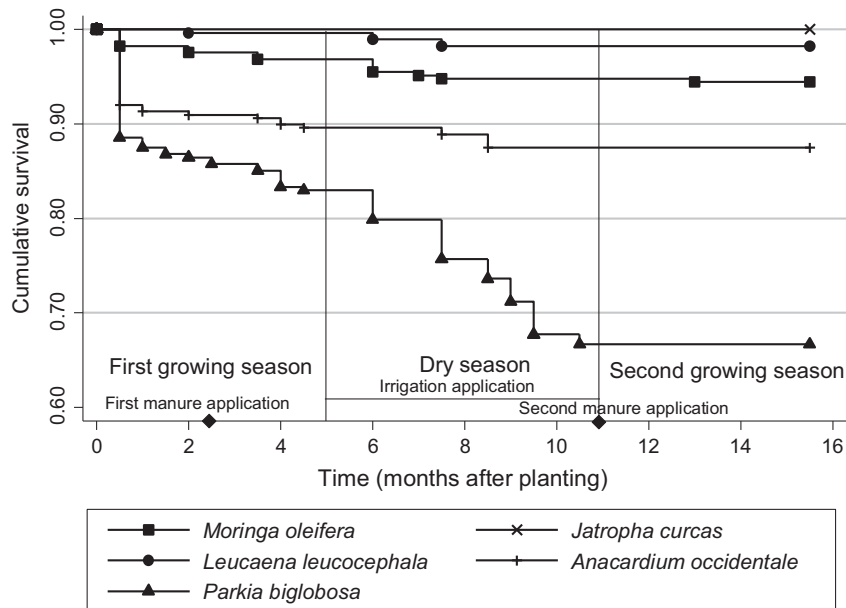


Fig. 3. Survival curves of five tree species during the first 15 months after planting in Northern Benin delineated according to the rainy (2) and dry (1) seasons, and when subjected to irrigation and manure applications.

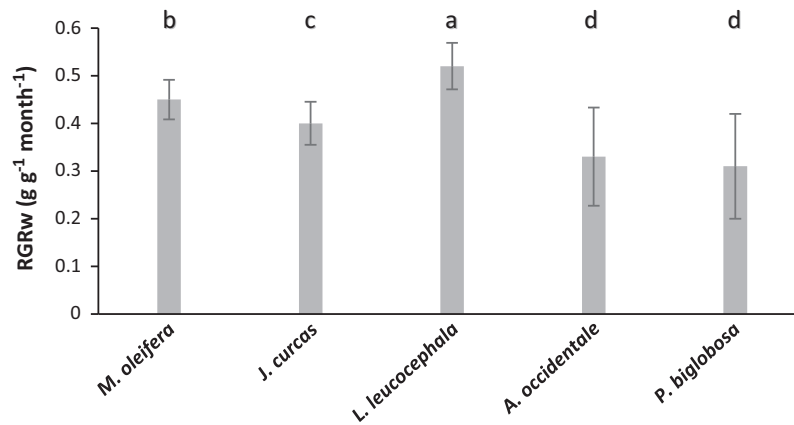


Fig. 4. Mean relative growth rate of whole-plant biomass (RGR_w) for five multi-purpose tree species computed for the period between the initial (MaP = 0) and the final monitoring point (15 MaP) across treatments. The vertical bars indicate the standard error (SE) of the mean, which is multiplied by 10 for improved visualization. Different letters indicate significant differences between species at $p < 0.05$ based on an LSD post hoc test.

species, *L. leucocephala* had the highest RGR_w , followed by *M. oleifera*.

3.3. Shoot-level traits

Species differed in all shoot-level traits over time (Table 3). *M. oleifera*, *J. curcas*, and *L. leucocephala* had the highest D and H followed by *A. occidentale* and *P. biglobosa*. This species order was maintained at 5, 11 and 15 MaP (Table 4). A similar ranking was observed for RGR_D and RGR_H at 5 and 15 MaP, for which *M. oleifera*, *J. curcas* and *L. leucocephala* had significantly higher growth rates than *A. occidentale* and *P. biglobosa* (Tables 3 and 4). In contrast, at 11 MaP, after the dry season, faster growth in D and H was recorded for *P. biglobosa* and *A. occidentale* than for the other three species.

Fertilization significantly increased the D and H for all species and assessment periods except for H at 11 MaP (Table 3). This growth-enhancing effect was most obvious at 15 MaP (Table 4). Similarly, RGR_D and RGR_H significantly increased with fertilization,

but decreased over the assessment period with the lowest rates observed at 11 MaP (Tables 3 and 4). The positive impact of irrigation was seen in the increased RGR_H at 15 MaP only.

Variation in D and RGR_D in response to fertilization differed between species and over time (at 5 and 11 MaP; Table 3). At 5 MaP, the increase in D in response to fertilization was significantly greater for *M. oleifera*, *J. curcas*, *L. leucocephala*, and *P. biglobosa* than for *A. occidentale*. At 11 MaP, manuring enhanced stem growth significantly in *P. biglobosa* (reflected in D and RGR_D) and *A. occidentale* (reflected in RGR_D ; see also Supporting Information Figs. S1a A and S1b A and C). Fertilization significantly increased sapling height in all species except *M. oleifera* at 15 MaP (Supporting Information Fig. S1c D). The effect of irrigation on shoot traits differed between species, predominantly at 15 MaP. Irrigation significantly increased D, RGR_D and RGR_H in *J. curcas* after supplemental irrigation (at 11 MaP) and at the end of the rainy period (15 MaP). Also, *P. biglobosa* was taller due to irrigation ($p < 0.05$) as measured at 15 MaP. In contrast, at the end of the observation period, irrigated *L. leucocephala* saplings were noticeably lower in terms of D and

Table 4
Effect of tree species, fertilization, and irrigation on the shoot (D, H, RGR_D, RGR_H) and root (RD, RE, RGR_{RD}, RGR_{RE}) traits of five tree species for three assessment periods over the first 15 months after planting (MaP). Means are expressed per tree, with an initial stand density of 5000 stems ha⁻¹.

Factors	Variables	Shoot-level traits											
		Basal diameter (D, cm)			Height (H, m)			Relative growth rate in diameter (RGR _D , cm cm ⁻¹ month ⁻¹)			Relative growth rate in height (RGR _H , m m ⁻¹ month ⁻¹)		
		5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP
Species	<i>M. oleifera</i>	4.55a	3.99b	6.90a	2.29a	2.59a	3.79a	0.56a	0.002c	0.135a	0.428a	0.021b	0.093b
	<i>J. curcas</i>	4.39a	4.32a	6.80a	1.08c	1.13c	1.44c	0.37b	0.004c	0.106cb	0.259b	0.010c	0.057c
	<i>L. leucocephala</i>	2.69b	2.68c	4.41b	1.85b	1.83b	3.05b	0.48c	0.013b	0.118ba	0.441a	0.009c	0.127a
	<i>A. occidentale</i>	1.82c	2.57c	3.79c	0.75d	1.01d	1.36c	0.20d	0.053a	0.096cb	0.137c	0.046a	0.074cb
	<i>P. biglobosa</i>	0.84d	1.51d	2.32d	0.33e	0.43e	0.80d	0.14e	0.083a	0.083c	0.045d	0.043a	0.138a
Fertilization	No fertilization	2.91b	3.10b	4.86b	1.30b	1.46a	2.10b	0.36b	0.022b	0.093b	0.273b	0.020b	0.084b
	Fertilization	3.15a	3.16a	5.51a	1.38a	1.48a	2.32a	0.38a	0.031a	0.127a	0.289a	0.028a	0.108a
Irrigation	No irrigation	n/a	3.31a	5.49a	n/a	1.58a	2.28a	n/a	0.023a	0.108a	n/a	0.019a	0.090b
	Irrigation	n/a	2.98a	4.95a	n/a	1.38a	2.15a	n/a	0.030a	0.111a	n/a	0.027a	0.101a
Root-level traits													
		Rooting depth (RD, m)			Maximum extent of lateral roots (RE, m)			Relative growth rate in rooting depth (RGR _{RD} , m m ⁻¹ month ⁻¹)			Relative growth rate in lateral root extension (RGR _{RE} , m m ⁻¹ month ⁻¹)		
		5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP	5 MaP	11 MaP	15 MaP
		Species	<i>M. oleifera</i>	0.34d	0.51cb	0.47d	1.15b	1.17b	1.62c	0.271bc	0.058 a	0.008b	0.026d
<i>J. curcas</i>	0.46b		0.56b	0.57c	1.27b	1.18b	1.83b	0.323a	0.032b	0.017b	0.748b	0.007b	0.099b
<i>L. leucocephala</i>	0.52a		0.65a	0.76a	1.69a	1.81a	2.41a	0.264b	0.038b	0.038a	0.803a	0.018ab	0.068d
<i>A. occidentale</i>	0.40c		0.46dc	0.56c	0.70c	0.64c	1.05d	0.191d	0.026b	0.048a	0.518c	0.017ab	0.122b
<i>P. biglobosa</i>	0.48ba		0.44d	0.66b	0.67d	0.89cb	1.75cb	0.293c	0.005c	0.092c	0.450c	0.049a	0.156a
Fertilization	No fertilization	0.43a	0.51a	0.60a	1.12a	1.25a	1.80a	0.266a	0.030a	0.038a	0.516a	0.023a	0.108a
	Fertilization	0.44a	0.55a	0.60a	1.15a	1.09b	1.70a	0.271a	0.037a	0.035a	0.511a	0.015b	0.093a
Irrigation	No irrigation	n/a	0.58a	0.58a	n/a	1.23a	1.77a	n/a	0.045a	0.027b	n/a	0.019a	0.092a
	Irrigation	n/a	0.49b	0.62a	n/a	1.13a	1.74a	n/a	0.024b	0.045a	n/a	0.019a	0.108a

n/a = not applicable. For each group of traits (shoot or root), the means with the same superscript within the same column are not significantly different at $p < 0.05$ between the species.

5 MaP covers the first growing season; during the dry season (5–11 MaP) supplemental irrigation was applied; 11–15 MaP covers the second growing season.

RGR_D compared to their non-watered counterparts (Supporting Information Figs. S2a A and S2b A and C).

The combined effects of fertilization and irrigation on shoot traits varied between species, mainly at 11 MaP (Table 3). As a general trend, the highest values for these traits were observed in saplings that were both fertilized and irrigated (data not shown).

3.4. Root-level traits

The species differed significantly in all their root-level traits across the three assessment periods and silvicultural treatments except for RGR_{RE} at 11 MaP (Table 3). *L. leucocephala* had the largest RE and RD overall, whereas variation between the other species was inconsistent, differing for RE, RD RGR_{RD} and RGR_{RE} (Table 4).

Fertilization and irrigation either enhanced or reduced root growth depending on the species and on the observation period (Tables 3 and 4). For all species, fertilization significantly decreased plant root elongation as measured by RE and RGR_{RE}, whereas watering reduced rooting depth (RD and RGR_{RD}) in saplings at 11 MaP (Table 4). At 5 MaP, greater root elongation (RE) was observed in manured *P. biglobosa* saplings but fertilization reduced RE and RGR_{RE} in *A. occidentale* ($p < 0.05$). Root elongation decreased significantly in *M. oleifera*- and *P. biglobosa*-manured saplings at 11 MaP (Supporting Information Figs. S1a F and H and 1b F). At 15 MaP, RE increased due to supplemental irrigation in *M. oleifera*, *A. occidentale* and *P. biglobosa*, but decreased in *L. leucocephala* ($p < 0.05$; Supporting Information Fig. S2b F). Variations in RD due to fertilization and irrigation treatments remained the same for all species.

The interaction effects of fertilization and irrigation on root elongation (RE and RGR_{RE}) differed between species at 11 and 15 MaP (Table 3). The smallest RE was observed in fertilized and

watered *M. oleifera* saplings, while the largest RE and RGR_{RE} were recorded in unfertilized and irrigated *P. biglobosa* saplings (data not shown).

3.5. Intra-specific trait plasticity in response to treatments

Intra-specific trait plasticity differed between the traits, as evidenced by the coefficient of variation (CV) across treatments ($P < 0.001$; Fig. 5). However, the difference in intra-specific trait variation at the shoot level vs. the root level was not significant ($P > 0.05$). RGR demonstrated the greatest variation in response to differences in resource availability across the three assessment periods, with root-level traits (RGR_{RD} and RGR_{RE}) being the most plastic. No significant differences between the two classes of tree species were observed for RGR, but the slow-growing species exhibited a greater plastic response in terms of the absolute indicators of above- and belowground growth (e.g. D, H and RE) than the fast-growers (Fig. 5). The exception was the RD, which was very likely restricted by the shallow soil and lateritic concretion at the afforestation site.

4. Discussion

4.1. Effects of nutrient and water supply on trait expression and plasticity

In accordance with earlier findings on tree saplings and seedlings from temperate and tropical regions (Funk et al., 2007; Barbosa et al., 2014; Coyle and Coleman, 2005) and mature trees from temperate areas (Coyle et al., 2016), the supply of nutrients and water enhanced the development of the shoot traits, as con-

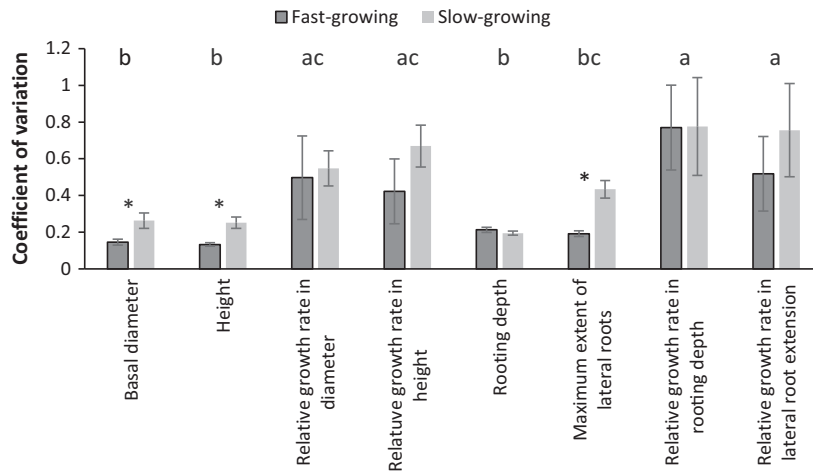


Fig. 5. Coefficient of variation (CV) across treatments and assessment periods as a proxy for the shoot and root level plasticity in response to varying resource availability. Shown are means for five tree species (*M. oleifera*, *J. curcas*, *L. leucocephala*, *A. occidentale*, and *P. biglobosa*). Vertical bars indicate the standard error (SE) of the mean. Different letters indicate significant differences between the traits and (*) indicates significant differences between fast- and slow growing species, all at $p < 0.05$ based on an LSD post hoc test.

firmly by the increased D and H in our trial. In the roots, a smaller RE in fertilized saplings and deeper rooting systems in non-irrigated saplings were observed in response to the treatments (Table 3), the latter trend a well-established belowground adaptation to drought stress (Mainiero and Kazda, 2006; Poorter et al., 2012). These findings are consistent with the hypothesis of functional resource allocation (Brouwer, 1963; Poorter et al., 2012), given that the saplings invested in root development to aid in the uptake of limiting resources, i.e. water and nutrients.

Fertilization- or irrigation-driven plastic changes were evident in all of the traits monitored, but the size of the variation in these traits differed between the shoots and the roots. For instance, RGR was the most plastic characteristic for all species (Fig. 5) and consequently can be considered a suitable indicator of the growth potential and performance of woody species in the long term. The importance of RGR as an early indicator of potential growth performance has been shown in numerous laboratory studies (e.g. Shipley, 2000) and a few field trials (e.g. Lamers et al., 2006). Our results indicate that the importance of RGR as a functional trait persists for woody species in an environment characterized by limited water and nutrient resources. Intra-specific variation in RGR was greatest in those root traits related to water and nutrient uptake (i.e., RD and RE), which could be due to the strategy of maintaining functional equilibrium at varying levels of resource availability (Brouwer, 1963; Poorter et al., 2012).

4.2. Species-related responses to nutrient and water supply

We can further describe plant responses to resource availability for two categories of tree species that were able to be identified based on RGR estimates averaged across the entire observation period (Fig. 4): (i) fast-growing *L. leucocephala*, *M. oleifera* and *J. curcas*, and (ii) slow-growing *A. occidentale* and *P. biglobosa*. The fast-growing species were characterized by more pronounced shoot development compared to the slow growers during both rainy seasons. However, in the dry season, slow growers exhibited greater development aboveground than did the fast growers due to the conservative use of resources, resulting in the improved performance of these slow-growing species even when resources are scarce (Reich, 2014). The studied species were grouped into fast and slow growers in accordance with their general characteristics, which are summarized in Table 1, as determined by a literature review (Edinger and Kaul, 2003; Maes et al., 2009; Fern, 2014).

During both growing seasons, the saplings of the fast-growing species invested more in the development of shoot traits under more fertile (manured) soil conditions. This reflects the high inherent plasticity in the shoot traits of these species during the rainy/growing seasons and supports the hypothesis of exploitative resource use and better responsiveness to increased nutrient availability according to the ‘fast-slow’ plant economics theory (Chapin, 1980; Reich et al., 2003b).

The response of slow-growing *A. occidentale* and *P. biglobosa* to organic fertilization was reflected in both the shoots and roots. For instance, non-manured *A. occidentale* saplings demonstrated greater RE and RGR_{RE} in the very early stages of growth (5 MaP) but, by the end of the observation period, these plants had greater shoot growth (indicated by greater RGR_H) due to an increased nutrient supply. The other slow-grower, *P. biglobosa*, had greater RE in manured plots at 5 MaP and in non-manured plots at 11 MaP, which was accompanied by elevated shoot growth (RGR_H) at 15 MaP. Unlike the fast-growers, these two species invested more in their root system, a known adaptation to nutrient stress (Khurana and Singh, 2001; Franko et al., 2006), thus demonstrating their ability to interact with spatial heterogeneity in soil fertility (Pérez-Harguindeguy et al., 2013) as a measure to acquire more nutrients. Furthermore, both slow-growers were more responsive in their shoot traits (D and RGR_D) to manuring during the dry season, evidence of their enhanced plastic response to treatments in both the shoot- and root level traits compared to the fast-growers (Fig. 5). This is very likely a direct consequence of their improved performance under low-resource conditions, as previously suggested (Siebenkäs et al., 2015; Reich, 2014).

Irrigation during the dry season markedly increased the survival of slow-growing *P. biglobosa*, but no clear differentiation could be made between fast and slow growers with regard to the effect of irrigation on their functional traits. Species responses to water supply were evident in the post-treatment period (11–15 MaP), suggesting a time lag; the lasting impact of irrigation was also observed in a drip irrigation trial with trees in arid Uzbekistan (Khamzina et al., 2008). The effect of irrigation was mirrored in the increased shoot growth in *J. curcas* and the development of a more extensive rooting system (reflected in RE) in *M. oleifera*, *A. occidentale* and *P. biglobosa*. The greater RE and stem growth (H) observed in non-watered *L. leucocephala* saplings at 15 MaP may be considered proof of their sensitivity to drought preconditioning, which resulted in improved above- and belowground performance during the second growing season (Vilagrosa et al.,

2003; Guarnaschelli et al., 2006). In general, the transplantation of seedlings from the nursery to the field may have caused additional stress, which is usually reflected in a shift towards increased root growth (Lyr and Hoffmann, 1967).

When all of the factors are considered, we can conclude that, as a consequence of the combined effects of manure and water application, both slow- and fast-growing woody species strongly improve their aboveground development. In contrast, the greatest improvement belowground was induced by the supply of manure to fast-growing species (e.g. *M. oleifera*) and water to slow-growing species (e.g. *P. biglobosa*).

4.3. Species choice and silvicultural management for the afforestation of degraded cropland

The judicious selection of multi-purpose tree species for use in the afforestation of degraded croplands in West Africa demands awareness of the species' ability to respond and adapt to the environmental stress imposed by water and nutrient deficits. Thus, suitable woody species should possess a set of features that allow them to tolerate these stressors, such as a high survival rate, quick growth, and an effective response to the water and nutrient supply. The vigor of five woody species on degraded cropland in Northern Benin was demonstrated in this paper by their generally (very) low overall incidence and high survival rates. In particular, over 15 months, *J. curcas* demonstrated a 100% survival rate, in line with previous reports, thus underlining the fact that the drought-resistance of this species enables its ready establishment on marginal lands in arid and semi-arid conditions (Francis et al., 2005; Maes et al., 2009; Reubens et al., 2011; Contran et al., 2013). However, failure has been reported when *J. curcas* plants are directly seeded in shallow soils with poor water holding capacity (Sop et al., 2012) or in the absence of silvicultural activities during the post-seedling growth stage (Baumert et al., 2014). The drought-tolerant *L. leucocephala*, whose seedlings have been reported to survive extended periods of dry soil and weather conditions (Shelton and Brewbaker, 1994), demonstrated strong growth in Benin as well. The observed mortality peak at 0.5 MaP for *M. oleifera*, *A. occidentale*, and *P. biglobosa* may be due to the stress caused by the transplantation of seedlings from the nursery.

Additional mortality peaks occurred during the dry season (Fig. 3), confirming that water stress is a primary cause of seedling mortality (Khurana and Singh, 2001). In support of previous findings (e.g. Bouda et al., 2013), our results found that *P. biglobosa* was the most susceptible to drought stress, as evidenced by the increased mortality in non-irrigated plants compared to their irrigated counterparts. Hence, extending the habitat range of these species to marginal croplands may be possible through supplemental irrigation. The advantages of irrigation applied during the first dry season after transplantation have been reported previously (e.g. Aerts et al., 2007) for *Olea europaea* spp. *cuspidata* grown in semi-arid, degraded savanna in Ethiopia. However, the adoption of irrigation practices even for commercially important tree crops in sub-Saharan Africa can be constrained by socio-political conditions and the lack of capital (Baumert et al., 2014).

Given the known investment risks for small-holder farmers, plantations of fast-growing *L. leucocephala*, *J. curcas* and *M. oleifera* may offer the greatest pay off. These species offer high early survival rates, growth rates, and plasticity in the aboveground organs in the presence of manuring and irrigation, which lower the abiotic stresses characteristic of degraded croplands. When manure is inaccessible or not available, planting *A. occidentale* and *P. biglobosa* is an option because both species exhibited a high plastic response to resource availability in above- and belowground organs during both the dry and rainy seasons. The mixed cultivation of fast and slow growers (e.g. Khamzina et al., 2006) could help diversify the

risks and increase the benefits of tree plantations on degraded croplands. In this respect, further studies should reveal a longer-term development of the established tree stands as well as management and harvesting approaches, such as thinning and pruning to reduce pest attack, allow for intercropping with cereals, etc. (Garrity et al., 2010; Baumert et al., 2014), that would therefore enhance benefits from afforestation.

5. Conclusion

This study on the use of functional traits to characterize the growth patterns of promising tree species introduced to degraded croplands and their responsiveness to silvicultural treatments in Northern Benin found that all five tree species were able to establish under water- and nutrient-limited conditions. Nevertheless, the species differed in survival rate due to their varying responses to drought, and exhibited differences in shoot and root morphological traits in the presence of both fertilization and irrigation. The most common response to the cultivation treatments was the enhanced growth of shoots in both fast- and slow-growing species across the dry and growing seasons, with the slow-growers performing better than the fast-growers during the dry season. The highest yield potential on degraded croplands was observed in the fast-growing *L. leucocephala*, *J. curcas* and *M. oleifera*, as reflected in the responsiveness of their aboveground growth to silvicultural management. In contrast, the slow-growing *A. occidentale* and *P. biglobosa* demonstrated greater adaptive ability in the face of nutrient stress. Therefore, a mix of fast and slow growers may promote the long-term productivity of plantations on degraded cropland. In particular, the relative growth rate (RGR) of each plant as a whole (i.e. shoots and roots combined) was a suitable indicator of growth performance, thus suggesting its possible application in the selection of tree species to be used in afforestation efforts. As both morphological and physiological processes determine plant growth, a consideration of those functional traits related to carbon assimilation and biomass allocation in the later growth stages of tree plantations is needed in the future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.11.018>. These data include Google maps of the most important areas described in this article.

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Electronic supplementary materials for Noulèkoun et al. (2017a)

Shoot and root responses of woody species to silvicultural management for afforestation of degraded croplands in the Sudano-Sahelian zone of Benin

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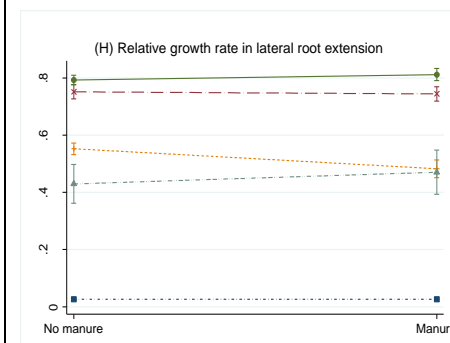
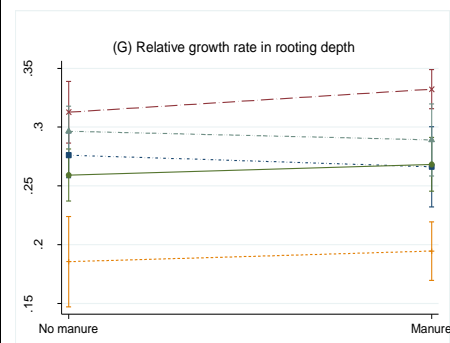
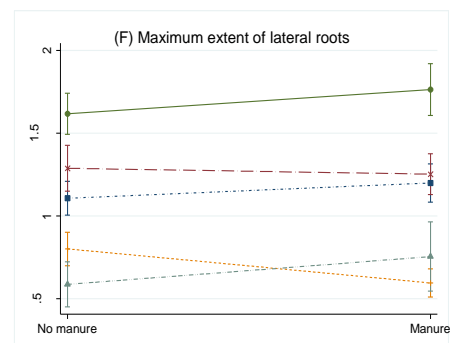
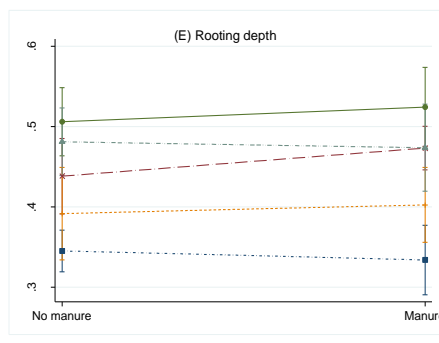
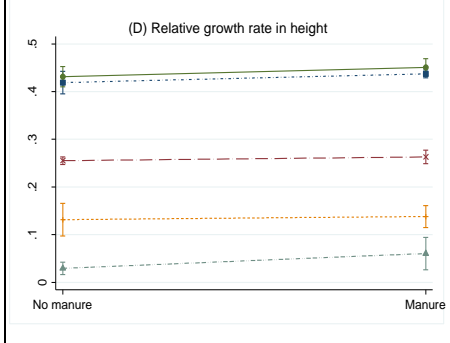
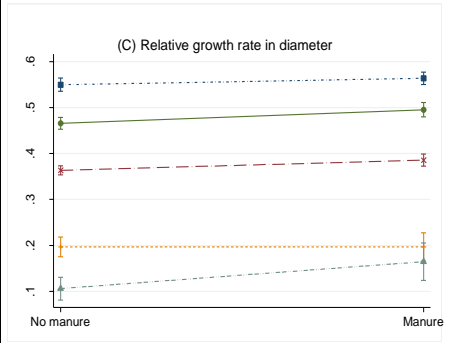
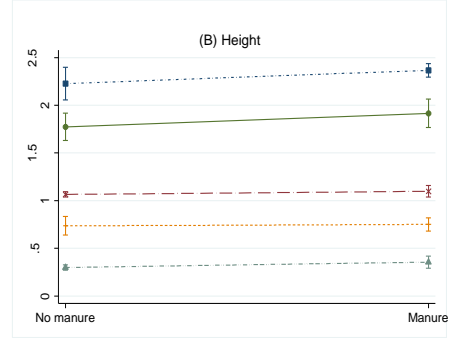
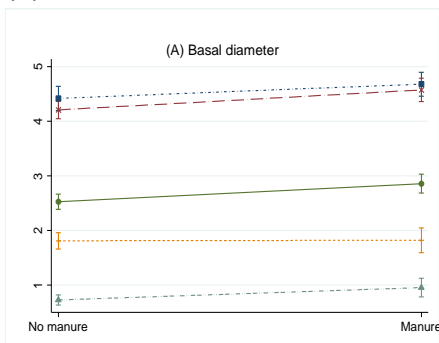
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Table S1 Soil physical and chemical properties at the study site in the Atacora region, northern Benin, at the beginning of the experiment in June 2014

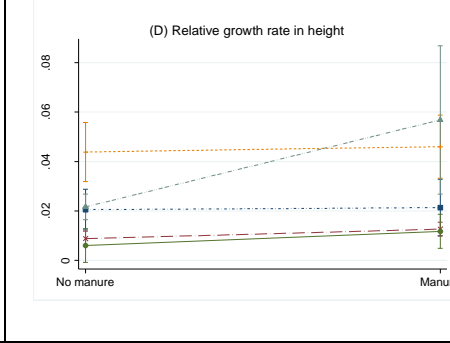
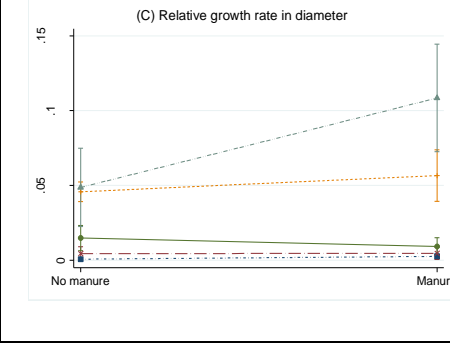
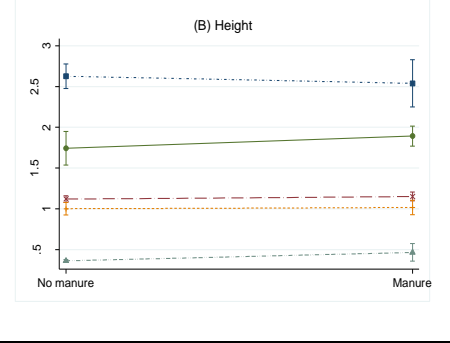
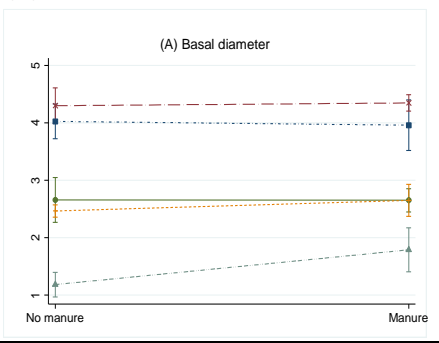
Parameter	Unit	Soil horizon (cm)			
		0-5	5-16	16-30	30-50
Texture	-	Sandy loam	Loam	Loam	Clayey loam
Clay	%	11.8	15.7	25.5	29.4
Silt	%	31.4	35.3	33.3	37.3
Sand	%	56.9	49.0	41.2	33.3
BD	g cm ⁻³	1.5	1.5	1.6	1.6
pF 2.5	% vol	7.8	10.9	13.4	15.9
pF 4.2	% vol	3.8	5.3	4.5	4.8
Ksat	Cm d ⁻¹	73.2	18.4	207.7	232.4
OM	%	1.2	1.1	1.1	0.9
C	%	0.7	0.6	0.6	0.6
N	%	0.1	0.1	0.1	0.1
C/N	-	12	12	13	13
P	mg kg ⁻¹	15.7	15.3	14.5	14.8
Kav	mg kg ⁻¹	90.7	77.6	16.1	20.2
Ca²⁺	cmol kg ⁻¹	2.5	2.7	2.9	2.1
Mg²⁺	cmol kg ⁻¹	0.9	1.9	1.7	2.9
K⁺	cmol kg ⁻¹	0.1	0.1	0.1	0.1
Na⁺	cmol kg ⁻¹	0.1	0.1	0.1	0.1
CEC	cmol kg ⁻¹	4.7	6.0	5.2	5.3
pH-H₂O	-	5.3	5.2	5.7	5.8

Legend: BD: bulk density; pF2.5: field capacity; pF4.2: permanent wilting point; Ksat: saturated hydraulic conductivity; OM: organic matter; C: carbon; N: nitrogen; Pav: available phosphorus; Kav: available potassium; CEC: Cation Exchange Capacity

(a) 5MaP



(b) 11MaP



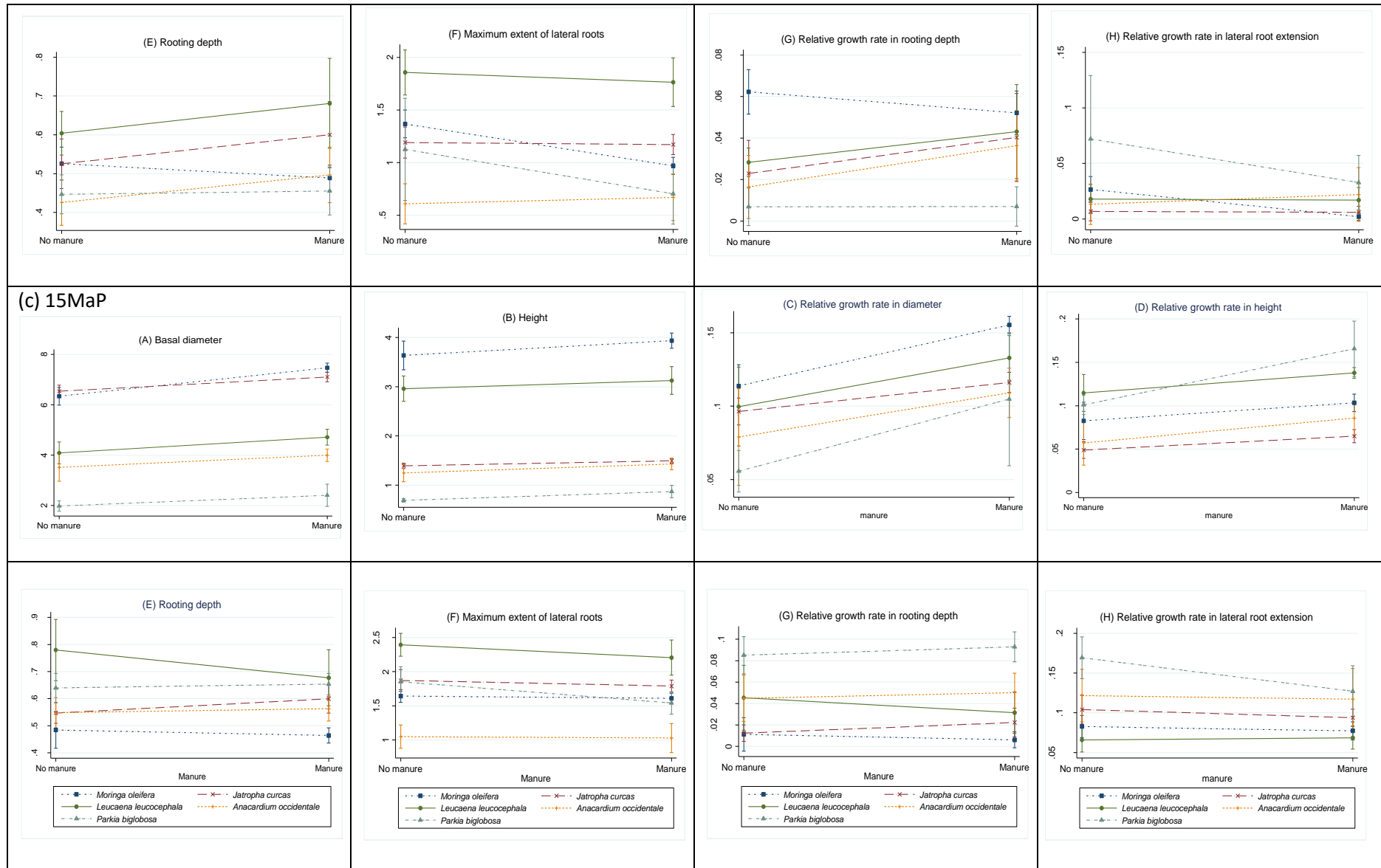
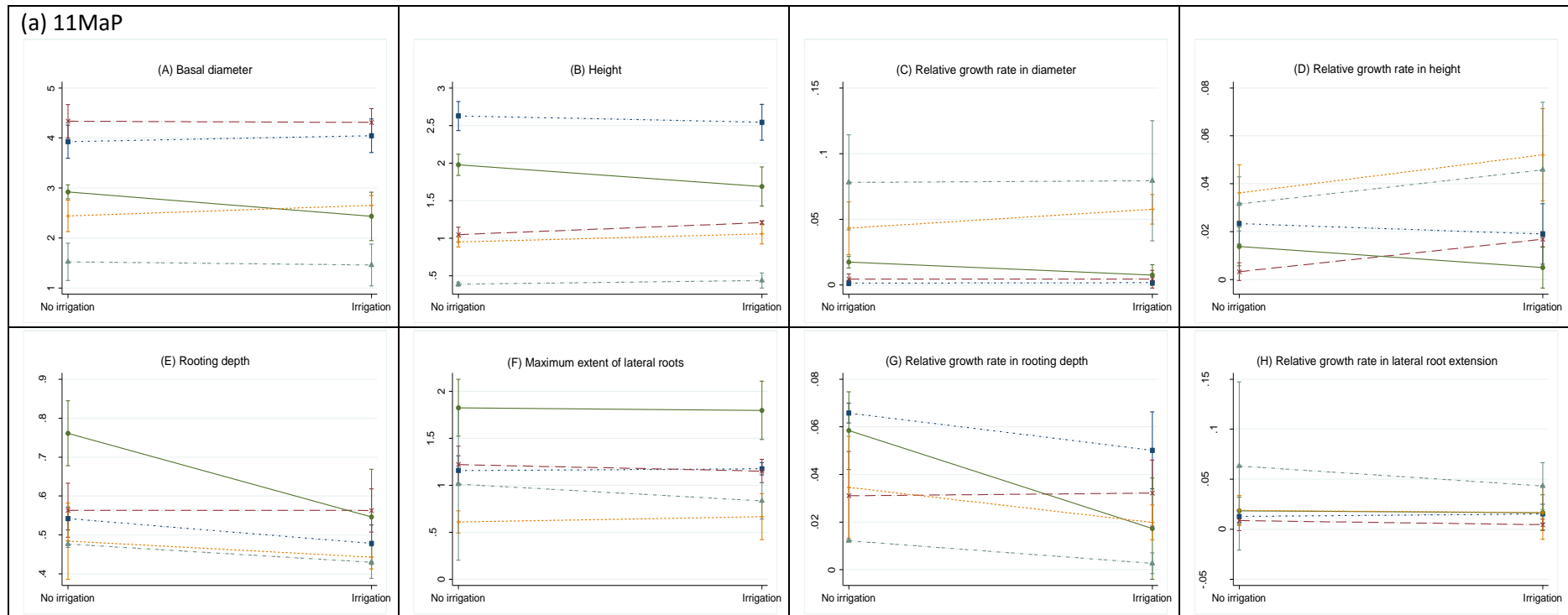


Figure S1 Shoot- and root-level traits of five multi-purpose tree species during the first 15 months after planting (MaP): a=5 MaP, b=11 MaP and c=15 MaP in response to fertilization (no manure and manure application). Shown are species predicted mean values (\pm 1 standard error of mean (SE) represented by vertical bars) across different levels of irrigation



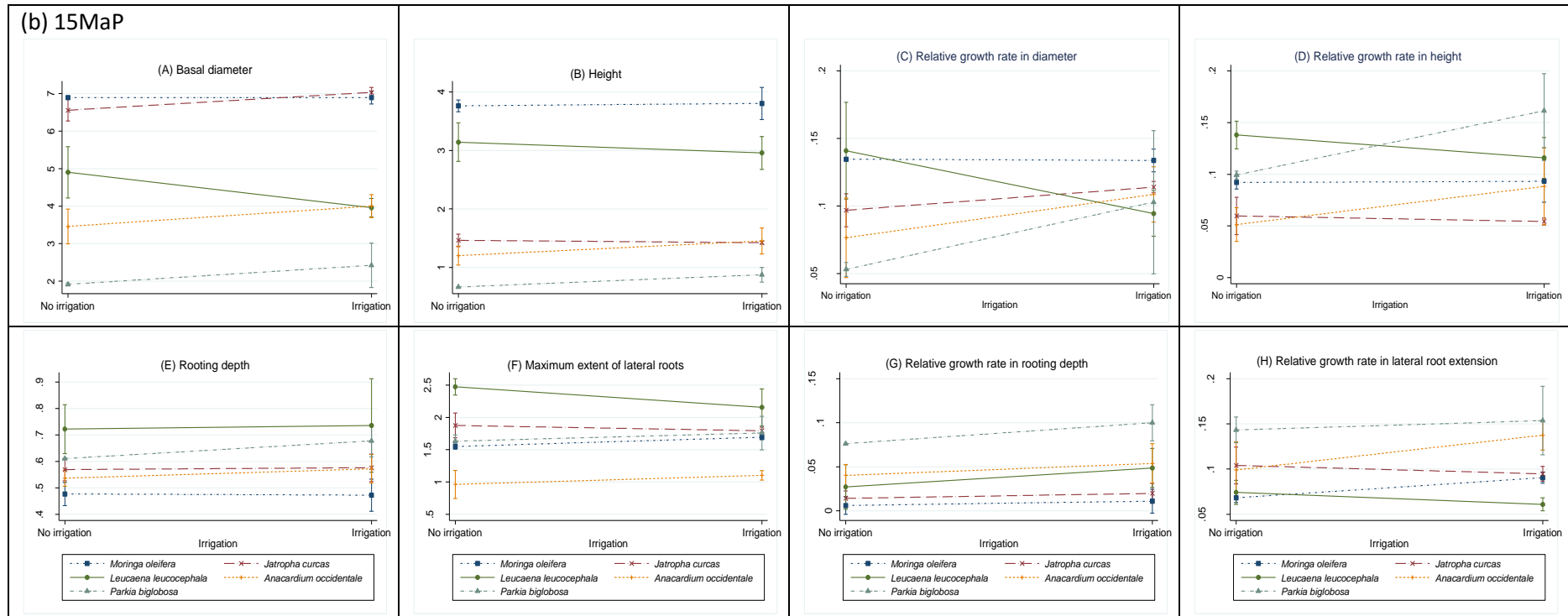


Figure S2 Shoot- and root-level traits of five multi-purpose tree species during the first 15 months after planting (MaP): a=5 MaP, b=11 MaP and c=15 MaP in response to no irrigation and irrigation. Shown are species predicted mean values (± 1 standard error of mean (SE) represented by vertical bars) across different levels of fertilization



Biomass allocation in five semi-arid afforestation species is driven mainly by ontogeny rather than resource availability

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Abstract

• **Key message** The changes in the relative biomass allocation to roots in juvenile stands of fast-growing (*Leucaena leucocephala* Lam., *Moringa oleifera* Lam., and *Jatropha curcas* L.) and slow-growing (*Anacardium occidentale* L. and *Parkia biglobosa* Jacq.) afforestation species are driven mainly by ontogeny rather than resource availability. However, silvicultural management aiming at increasing availability of water and particularly nutrients enhances biomass production in all species.

• **Context** Understanding the patterns of biomass allocation among tree species in response to ontogeny and to variation in resource availability is key to the successful restoration of degraded land using forest plantations.

• **Aims** This study assessed the effects of resource availability and ontogeny on biomass accumulation and partitioning in five semi-arid afforestation species.

• **Methods** The aboveground and belowground biomass production of fast-growing *Leucaena leucocephala* Lam., *Moringa oleifera* Lam., and *Jatropha curcas* L. and slow-growing *Anacardium occidentale* L. and *Parkia biglobosa* Jacq. was monitored following the application of manure (1 kg plant⁻¹) and/or supplemental irrigation (0.5 L per sapling daily) during the first two rainy seasons and the intervening dry season on degraded cropland in Northern Benin.

• **Results** Biomass accumulation in the fast-growing species was positively impacted by fertilization and irrigation during both rainy seasons. The slow-growing species responded positively to the silvicultural treatments during the dry and second rainy season. The application of fertilizer alone increased the biomass of *P. biglobosa* by up to 335% during the dry season. Fifteen months after planting, manure-treated *L. leucocephala* accumulated the most biomass (2.9 kg tree⁻¹). The root fraction decreased with increasing tree size in all species. The comparison of root versus shoot allocation in trees of equal size indicated that the treatment-induced shifts in biomass partitioning were controlled by ontogeny, which explained 86–95% of the variation in root-shoot biomass relationships.

• **Conclusion** While ontogeny was the main driver of biomass partitioning, increased resource availability induced a larger production of biomass, overall leading to greater aboveground production in all species.

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Contribution of the co-authors All authors conceived and designed the experiment. FN and JBN collected the field data. FN performed statistical analyses and composed the manuscript. AK, JBN, and JPAL contributed to the development of the manuscript.

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Keywords Intensive silviculture · Manuring · Drip irrigation · Roots · Optimum partitioning theory

1 Introduction

Conserving and restoring natural forests is essential in coping with the growing demand for timber and non-timber forest products and ensuring environmental sustainability in tropical regions (Steege et al. 2015). In sub-Saharan Africa (SSA), these efforts are increasingly constrained by the decline in the per capita availability of agricultural land (de Graaff et al. 2011), required to satisfy the food, feed, and fuel demands of the ever-increasing population. The resulting pressure on marginal land (Azuka et al. 2015) has dramatically reduced the duration of fallows, the traditional practice used to restore soil fertility (Nandwa 2001). The increasing variability

of rainfall in SSA (Sylla et al. 2016) has become an additional obstacle for efforts to improve cropland productivity and regenerate forest areas. In this regard, the afforestation of degraded cropland and intercropping with multi-purpose tree species offer the possibility of increasing on-farm tree cover, reversing land degradation, and contributing to rural livelihoods (Chamshama and Nduwayezu 2002; Garrity et al. 2010; Khamzina et al. 2012).

Though afforestation is a promising strategy, nutrient and water limitations on degraded land may hamper its success. Intensive silviculture, including fertilization, irrigation, pest control, and weed control, has been successful in overcoming environmental constraints and increasing forest production (e.g., Fening and Gershenson 2002; Mead 2013; Coyle et al. 2016). However, this is yet to be adopted in most dryland afforestation systems due to insufficient incentives for farmers to invest in ecological restoration (e.g., Djalilov et al. 2016) but is practiced for tree species of commercial importance, such as *Jatropha curcas* L. in biofuel production (Baumert et al. 2016). For instance, fertilization alone mitigated the negative effects of nutrient stress, resulting in enhanced stem growth (6–30%) in *J. curcas* and *Parkia biglobosa* Lam. saplings on nutrient-poor soils under semi-arid conditions (Noulèkoun et al. 2017) and greater aboveground biomass (AGB) accumulation (125–200%) in two 3-year-old *Populus deltoides* genotypes in a temperate climate (Coyle and Coleman 2005). Irrigation also improved tree productivity under scarce and erratic rainfall (Khamzina et al. 2008; Trichet et al. 2008; Noulèkoun et al. 2017). Early growth responses of trees to silvicultural treatments are reflected in the adjustment of biomass partitioning between roots and shoots. This relative allocation of biomass can be indicative of the physiological potential and long-term growth trajectory of tree species (e.g., Niklas 1994; McConnaughay and Coleman 1999; Reich 2002; Lamers et al. 2006). Critical physiological processes regulating resource acquisition and plant growth under nutrient and/or water stress occur belowground (Coyle and Coleman 2005). Hence, the root share can account for a substantial portion of total biomass (27–68%) in (sub-)tropical dry forests or plantations (Mokany et al. 2006).

Variations in belowground biomass (BGB) proportions during tree growth are controlled by both resource availability and development (i.e., ontogeny) (Coyle et al. 2008, 2016). Increased resource availability (e.g., nutrient and water) enhances AGB accumulation (which is usually of interest to farmers) as a result of allocation shifts from root to shoot (e.g., Albaugh et al. 1998; McConnaughay and Coleman 1999; Coleman et al. 2004; Coyle et al. 2016). Changes in the relative biomass allocation to roots in

response to resource availability are predicted to accord with the optimum partitioning theory (OPT), which suggests that plants allocate more biomass to the organ that acquires the most limiting resource (Brouwer 1963; Bloom et al. 1985). However, studies comparing plasticity in root/shoot ratios at common plant size or development stage (not at common plant age or time) have suggested that the shifts in biomass partitioning cited in support of the OPT may largely be induced by accelerated development (e.g., McConnaughay and Coleman 1999; Coleman et al. 1994, 2004). Therefore, it is important to separate the dynamics of development-induced (i.e., ontogenetic drift) changes in biomass allocation from those modulated by silvicultural treatments (i.e., “true” plasticity in allocation) when identifying the controlling factors (McConnaughay and Coleman 1999; Reich 2002; Coleman et al. 2004).

Multi-species plant studies, aiming at distinguishing between biomass allocation changes that result from ontogenetic drift and true adjustment, are scarce in tropical climates, particularly in the context of the afforestation of degraded drylands. This is partly because the required sequential sampling of AGB and BGB is challenging in open-field research (Robinson 2004). We assessed biomass allocation patterns in five afforestation species grown on degraded cropland under varying levels of nutrients and water supply during early stand development in Northern Benin, West Africa. Three of the tested species (*Leucaena leucocephala* Lam., *Moringa oleifera* Lam., and *J. curcas*) were previously classified as fast-growing and two (*Anacardium occidentale* L. and *P. biglobosa*) as slow-growing species, based on the response of root-level and shoot-level morphological traits to nutrient and water amendments (Noulèkoun et al. 2017). Yet, the previous studies did not address the dynamics of plant aboveground and belowground responses to silvicultural treatments with emphasis on biomass production and allocation. We hypothesized that (i) increased resource availability boosts biomass production significantly more in species characterized by faster ontogenetic development than in slow growers, (ii) biomass partitioning to belowground decreases with ontogeny, and (iii) when ontogeny is accounted for as a function of plant size, increasing resource availability triggers greater biomass allocation to aboveground versus belowground.

2 Materials and methods

2.1 Study site description

The study site, plant materials, and experimental design were previously described in detail by Noulèkoun et al. (2017). The research was carried out in Pouri village (N 10° 54' 8.4" and E 1° 4' 47.4") located on the periphery of the Dassari catchment in the department of Atacora, Northern Benin. The area is

characterized by a semi-arid climate, marked by one dry season (November to March) with temperatures rising as high as 45 °C and one rainy season (April to October) with temperatures falling to 14 °C. The average annual precipitation for the 15-month study period, spanning the 2014 and 2015 rainy (growing) seasons, was 795 mm. The vegetation is typical for a Sudan savanna ecological zone, with parklands, forest patches, and agricultural and fallow land, all of which are impacted by human activity (Saïdou et al. 2004; Chabi et al. 2016). The soils are compacted, limited in their depth by gravel and lateritic formations, and have low to moderate inherent fertility (Saïdou et al. 2004; Azuka et al. 2015). The soil at the research site was classified as an epipetric plinthosol with sandy-loamy texture in the surface layer and loamy soil dominated by clayey loam in deeper layers. Total carbon and NPK measured 0.5%, 0.1%, 1.2 mg kg⁻¹, and 44.3 mg kg⁻¹, respectively.

2.2 Woody species

The afforestation trial established at the degraded cropping site in July 2014 included five (semi-)deciduous tree species that differed in terms of their growth potential and tolerance to drought (Noulèkoun et al. 2017): the fast-growing *Moringa oleifera* Lam. (drumstick tree, Moringaceae), *Jatropha curcas* L. (physic nut, Euphorbiaceae), and *Leucaena leucocephala* Lam. (leucaena, Fabaceae) and the slow-growing *Anacardium occidentale* L. (cashew, Anacardiaceae) and *Parkia biglobosa* Jacq. (African locust bean, Fabaceae). Seeds were germinated in a local nursery and planted at the experimental site after 2.5–4 months.

2.3 Experimental design

Three experimental factors were considered to influence plant growth and biomass production and allocation: (i) the five species and two silvicultural treatments consisting of (ii) drip irrigation and (iii) fertilization by manuring. The species and irrigation variables were subject to a fully factorial design with three repetitions, while manuring was nested within plots. The design thus consisted of a total of 30 pure species plots, each 12 × 8 m² in size. Each plot contained 48 seedlings spaced at 2 × 1 m, resulting in an initial density of 5000 plants ha⁻¹.

The irrigation and fertilization treatments resulted in four resource management options: no resource manipulation (control, C), irrigation (I), fertilization (F), and irrigation plus fertilization (IF). An adapted drip irrigation system (Fig. 1) was used during the dry season to supply 0.5 L of water per sapling daily to meet 30% of the evaporative demand (Allen et al. 1998). This amounted to a total of 72.5 mm of irrigation. In addition, saplings received 33 mm of rainfall during the 2014–2015 dry season. Manure was supplied in the amount of 1 kg per plant in both growing seasons, i.e., at 2.5 and

11 months after planting (MaP). The manure was composted cow and pig dung and contained on average 18.7% carbon (C), 1.2% nitrogen (N), and 0.8% phosphorus (P).

2.4 Biomass production

Plants were sampled at 5, 11, and 15 MaP, representing the first growing (rainy) season (0–5 MaP), the subsequent dry season (5–11 MaP), and the second growing season (11–15 MaP). At each sampling, two to six saplings were randomly selected from each experimental plot and harvested entirely. The plants were felled, and the AGB separated into leaves (including the petiole), stems with branches, and (if present) reproductive parts. Roots were manually excavated and sectioned into coarse ($\phi > 2$ mm) and fine ($\phi < 2$ mm) fractions. The roots were gently washed on a sieve and freed of soil. The fresh mass of each fraction was recorded in the field using a 7-kg portable scale (accuracy 0.1 g) and oven-dried at 75 °C until a constant weight. Woody samples were cut into small pieces before oven drying.

At 11 MaP, biomass was also sampled from a 10-year-old natural fallow, located in the vicinity of the experiment to compare biomass productivity between afforested (active intervention) and fallowed (natural succession) sites. An area of 0.5 ha was delineated in the fallow land where three sub-plots of 4 × 4 m each were installed along one of the diagonals for sampling. Grazing was not controlled. The AGB and BGB of the predominant vegetation, consisting of shrubs (e.g., *Combretum glutinosum*) and trees (e.g., *Terminalia macroptera*), were quantified for each species and sub-plot as described above.

2.5 Statistical analyses of treatments

A linear mixed-effect model was used to assess the effects of the abovementioned experimental factors on biomass production at 5, 11, and 15 MaP. The effect of irrigation was tested at 11 and 15 MaP. The statistical analyses consisted of several steps. First, the effects of species, treatment (F and I), and treatment interaction on total biomass production were tested. Second, differences observed between the species in biomass production with respect to the silvicultural treatments were analyzed. Species, fertilization, and irrigation were considered as fixed terms, while plot identity and fertilization (nested within plots) as random terms. The robust variance estimates and unstructured covariance options in STATA 14 (StataCorp 2015) were used to control for any deviation from the assumption of normality in the data. A least significance difference (LSD) test was used to compare means when significant treatment effects were found.

Fig. 1 Drip system using local 1.5-L plastic bottles for the supplemental irrigation of saplings during the dry season (December 2014–May 2015) at the afforestation site in Northern Benin



2.6 Relative biomass allocation analysis

The effect of the treatments and ontogeny on biomass allocation was evaluated using clasmometric and allometric analyses (Poorter and Sack 2012). For the clasmometric analysis, the root mass fraction (RMF) was computed and plotted against the natural log-transformed estimate of the whole-plant dry biomass, which was used as a reference for the ontogenetic stage (e.g., Evans 1972; Poorter and Pothmann 1992; Poorter and Sack 2012). The allometric analysis was performed using an approach that allows for the differentiation between the effects of ontogeny and resource availability on biomass allocation (Hunt 1978; Coleman et al. 2004):

$$\ln Y = a + k \ln X \quad (1)$$

where Y is the total root (coarse and fine) dry mass, X is the total shoot (leaf and stem) dry mass, a is the y intercept, and the slope k is the allometric coefficient. The greater the value of k , the greater the biomass allocation to the roots relative to the shoots. If k is similar between the treatments, any shift in biomass allocation can be attributed to development (Hunt 1978). An analysis of covariance (ANCOVA) was used to reveal differences in k between treatments. The ANCOVA consisted of fitting the model in Eq. 1 to the treatment class variable. A significant interaction between the covariates (natural log-transformed stand-level estimates of root and shoot dry mass) and the treatment variable is considered indicative of a treatment-induced shift in biomass allocation. An ANCOVA was also used to compare the RMF versus tree size relationship between the treatments as revealed by clasmometry. In the case of significant interactions between the covariate and treatment factor, an LSD post hoc test was used to compare the slopes. In the case of equality of slopes between the treatments, a test of differences in intercepts was additionally performed. Following Niklas and Enquist (2002) and Poorter et al. (2015), the reproductive biomass fractions (fruits of *J. curcas* and pods of *M. oleifera*), which represented 2–5% of the total biomass, were omitted from the analyses.

To further assess the relative explanatory power of ontogeny and treatment effects on biomass allocation, stepwise multiple regression was conducted to characterize the effect of total dry mass, fertilization, and irrigation on root dry mass separately for each species. The natural log-transformed mass values and their residuals were judged to be normally distributed and homoscedastic based on a combination of histograms and normality tests performed in STATA 14. Data from the three harvests at the experimental site were pooled to account for changes in biomass allocation over the full size range (Poorter et al. 2012; Poorter and Sack 2012).

3 Results

3.1 Biomass production

3.1.1 Effects of resource supply

The shoot, root, and total biomass were affected by fertilization and irrigation, but the effects differed between species and assessment periods (Table 1). At 5 MaP, total biomass increased due to fertilization (F) compared to the control (C) by 18% in *M. oleifera*, 23% in *J. curcas*, and 25% in *L. leucocephala*. No significant difference in biomass accumulation was observed between the C and F treatments for *A. occidentale* and *P. biglobosa* saplings, which were the smallest in size (Figs. 2a and 3a, Supplementary material, Appendix S1). The fertilizer-related biomass increase in fast-growing species was mirrored predominantly in AGB accumulation (Fig. 2, Supplementary material, Appendix S1). At the end of the dry season (11 MaP), only the slow-growing species responded to treatments (Table 1, Supplementary material, Appendix S1). Both *A. occidentale* and *P. biglobosa* saplings accumulated greater root biomass under IF and F compared to C at this point in time (Fig. 2b). The continued growth during the dry season substantially enhanced total biomass accumulation in *P. biglobosa*, which increased by 176% under IF and by 335% under F compared

Table 1 Significance of species, fertilization, irrigation, and fertilization \times irrigation factors for aboveground and belowground biomass production after the first growing season (0–5 MaP), the dry season (5–11 MaP), and the second growing season (11–15 MaP) for plantations of *M. oleifera*, *J. curcas*, *L. leucocephala*, *A. occidentale*, and *P. biglobosa* on degraded cropland in Northern Benin. *P* values lower than $\alpha = 0.05$ are indicated in italics

Factors	Shoot ^a	Root ^b	Total ^c
5 MaP			
Species (S)	< 0.001	< 0.001	< 0.001
Fertilization (F)	< 0.001	0.002	< 0.001
S \times F	0.002	0.021	0.005
11 MaP			
Species (S)	< 0.001	< 0.001	< 0.001
Fertilization (F)	0.549	0.915	0.677
S \times F	0.579	< 0.001	0.035
Irrigation (I)	0.918	0.716	0.838
S \times I	0.403	0.109	0.354
F \times I	0.873	0.019	0.583
S \times F \times I	0.082	< 0.001	< 0.001
15 MaP			
Species (S)	< 0.001	< 0.001	< 0.001
Fertilization (F)	< 0.001	< 0.001	< 0.001
S \times F	< 0.001	< 0.001	< 0.001
Irrigation (I)	0.183	0.827	0.281
S \times I	< 0.001	< 0.001	< 0.001
F \times I	0.253	0.002	0.114
S \times F \times I	0.832	0.104	0.711

^a Shoot = leaves + stem; reproductive parts were not included

^b Root = coarse roots + fine roots

^c Total = shoot + root

to C. In contrast, the total biomass of the fast-growing species declined between 5 and 11 MaP mainly due to a loss of shoot biomass (Fig. 2b). At the end of the second growing season (15 MaP), total biomass followed the order F > IF > I > C for the fast growers, although the differences between treatments were not statistically significant in all cases (Fig. 2c). For the slow growers, the pattern of treatment effects on total biomass followed the order of IF = F = I > C. The range of the increase in total biomass under F compared to C was substantially greater (8–335%) in the slow growers compared to that in the fast-growing species (19–68%). A significant effect of second-order interactions (e.g., species \times fertilization \times irrigation) was observed on root and total biomass at 11 MaP only (Table 1) but resulted from differential responses of fast-growing and slow-growing species to treatments (Fig. 2).

Fertilization consistently affected every biomass component at 5 and 15 MaP. Conversely, the overall effect of irrigation was marginal. It was much more evident at 15 MaP and varied greatly between species (Table 1, Fig. 2).

3.1.2 Species differences

At 5 MaP, the species ranking in terms of total biomass accumulation followed the order *M. oleifera* > *J. curcas* > *L. leucocephala* > *A. occidentale* > *P. biglobosa* (Fig. 3a). Shoot biomass ranking followed the same order, but the root biomass was similar for *A. occidentale* and *P. biglobosa*. At 11 MaP, total biomass did not significantly differ between *M. oleifera* and *L. leucocephala* and between *J. curcas* and *A. occidentale* (Fig. 3b). At 15 MaP, *L. leucocephala* accumulated significantly greater total biomass than the other four species while *A. occidentale* and particularly *P. biglobosa* accumulated the lowest total biomass (Fig. 3c). For instance, total biomass in *L. leucocephala* was 53% greater than in *M. oleifera*, 183% greater than in *A. occidentale*, and 659% greater than in *P. biglobosa*. Shoot and root biomass followed a similar pattern (Fig. 3c). The total biomass on the 10-year-old fallow land was estimated at 19.98 Mg ha⁻¹.

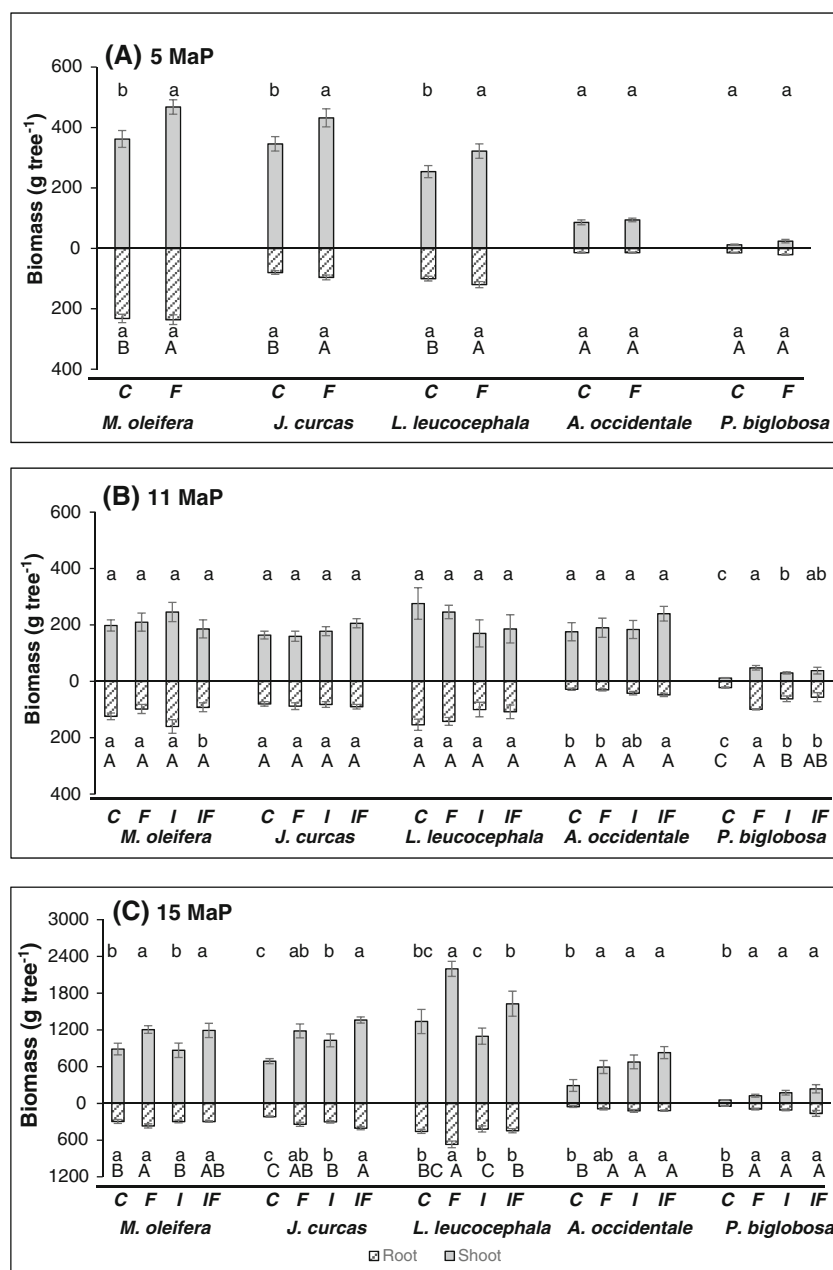
3.2 Biomass allocation

3.2.1 Effects of resource supply

For all species and treatments, the RMF fell (slope < 0, Fig. 4) with increasing tree size, reflecting ontogenetic drift, except in *A. occidentale*, which demonstrated no significant change ($P = 0.68$, Table 2, Fig. 4f). The decrease in RMF was influenced by the F and I treatments (Supplementary material, Appendix S2), but this exhibited great variation and was species specific (Fig. 4). For *M. oleifera*, the decline in the RMF was larger in saplings under C, I, and IF than in those under F, whereas a greater decrease occurred in *L. leucocephala* saplings under IF and I compared to C and F treatments (Table 2, Fig. 4a, c). However, treatment had no effect on the RMF in *J. curcas*, *A. occidentale*, or *P. biglobosa* ($P > 0.05$; Table 2).

Allometric analysis revealed significant and strong linear relationships ($R^2 > 0.8$) between root and shoot biomass (Table 3). For *J. curcas*, *L. leucocephala*, and *A. occidentale*, the variations in biomass allocation to belowground between treatments were all explained by ontogeny, as evidenced by a k that did not significantly differ between treatments (Table 3). The rate of increase in root biomass with increasing shoot biomass (i.e., k) did not differ ($P > 0.05$) between treatments for *P. biglobosa*, but the intercept was significantly higher for saplings grown under C and I compared to F and IF ($P = 0.038$; data not shown). Conversely, *M. oleifera* exhibited a significantly higher k under both F and IF compared to C and I treatments (Table 3), indicating that the treatments altered belowground allocation in this species. Due to the differing patterns of treatment-induced effects on the allometric relationship, the relative variation explained by ontogeny and by fertilization and irrigation was further distinguished. The ontogeny was always important in the allometric relationship between roots and shoots, explaining 86–

Fig. 2 Aboveground (leaves and stem) and belowground (coarse and fine roots) biomass of five woody species at **a** 5 MaP, **b** 11 MaP, and **c** 15 MaP on degraded cropland in Northern Benin. Treatments included control (C), fertilization (F), irrigation (I), and irrigation + fertilization (IF). The “zero” line on the y-axis delineates the ground surface. Vertical bars are standard errors of the mean. Lowercase letters above the bars denote shoots and those below the bars roots. Capital letters relate to total biomass. For each species, means with different letters indicate the significant impact of the treatment according to a LSD post hoc test ($\alpha = 0.05$)



95% of the variation in all species ($P < 0.001$, Table 4). The amount of variation in the root versus shoot allocation explained by fertilization was 0.3–0.7% and that by irrigation 1.4–43%. Neither factor appeared significant in the models (Table 4).

3.2.2 Species differences

Of the species selected for this study, the RMF was the highest in *P. biglobosa*, ranging between 30 and 75% of the total biomass over the entire size range (Fig. 4f). The proportion of total biomass allocated to belowground was $< 50\%$ in *M. oleifera*, *J. curcas*, and *L. leucocephala* and $< 30\%$ in *A. occidentale*. The latter had the highest k value of the five

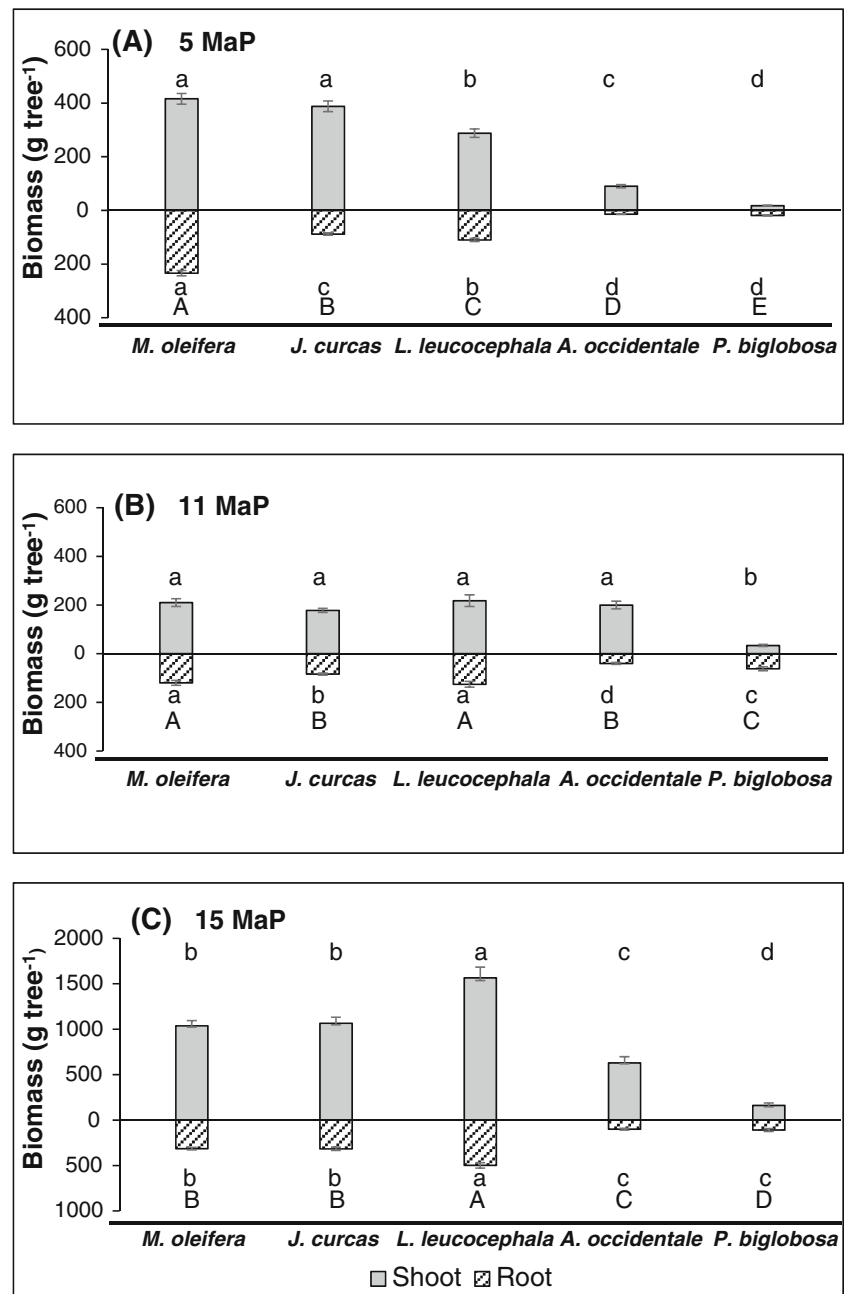
species, which was close to unity (a mean of 0.98 with a 95% confidence interval between 0.9 and 1.06, Table 3). The k values averaged 0.66 ± 0.09 , 0.78 ± 0.08 , 0.78 ± 0.07 , and 0.75 ± 0.07 for *M. oleifera*, *J. curcas*, *L. leucocephala*, and *P. biglobosa*, respectively (Table 3).

4 Discussion

4.1 Silvicultural treatment effects

The addition of manure and supplemental irrigation generally increased biomass production in the multi-species

Fig. 3 Mean aboveground (leaves and stem) and belowground (coarse and fine roots) biomass across treatments for five woody species at **a** 5 MaP, **b** 11 MaP, and **c** 15 MaP on degraded cropland in Northern Benin. Treatments and symbols are as in Fig. 2

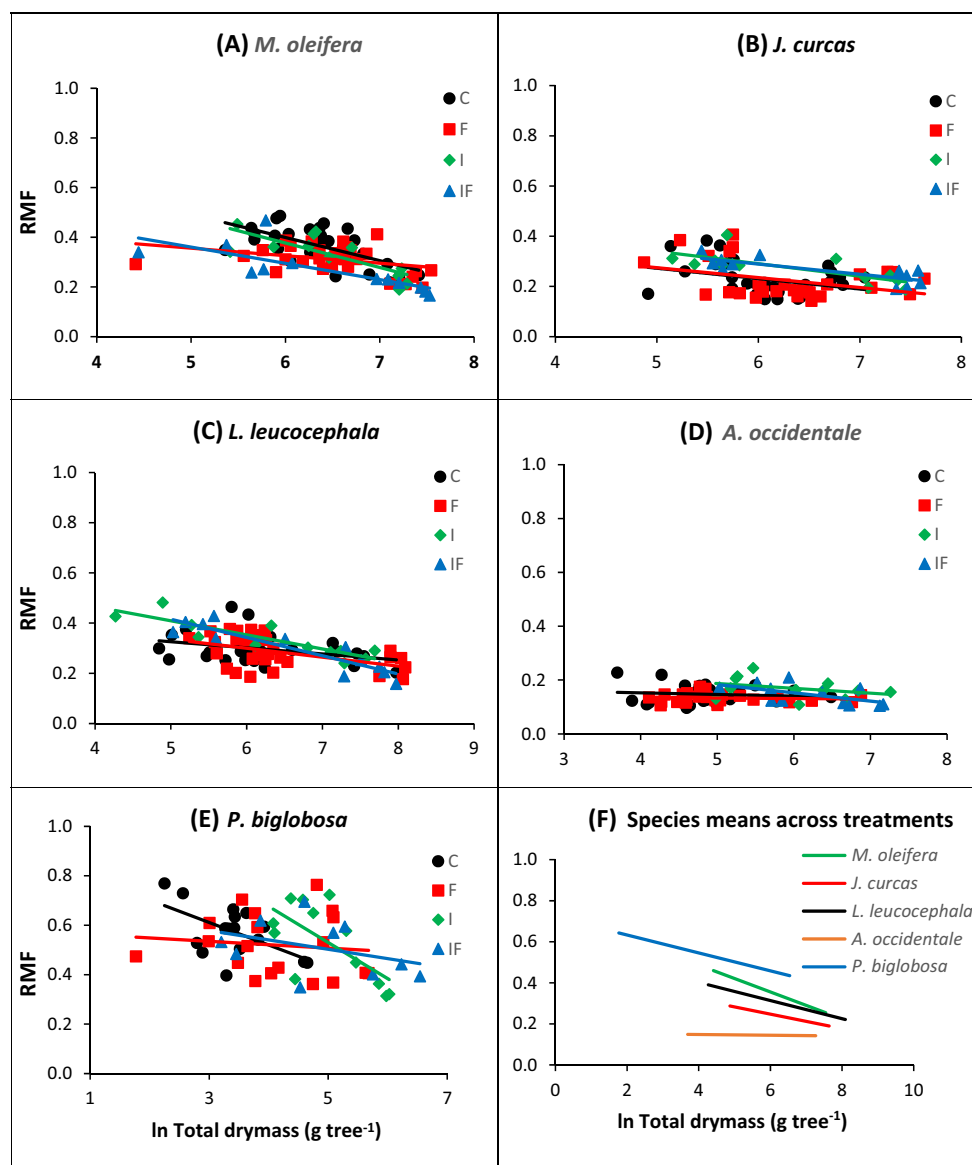


afforestation system. During the earliest stage of development (0–5 MaP) and in the second growing season (11–15 MaP), increased nutrient availability led to greater aboveground and total biomass accumulation but in *M. oleifera*, *J. curcas*, and *L. leucocephala* only. This confirms our hypothesis that increased resource availability has a more positive effect on the biomass production of fast-growing species than it does on slow-growing species. The higher sensitivity of the three fast-growing species to the experimental treatments is likely a result of their exploitative use of resources (Reich et al. 2003; Reich 2014; Noulèkoun et al. 2017). In contrast, both slow-growing species were responsive to silvicultural practices during the dry season (5–11 MaP), which is in line with

the hypothesis that increased resource availability also increases biomass production in slow growers. Fertilization and irrigation led to greater total biomass accumulation in *P. biglobosa* and to an increase in BGB in *A. occidentale* saplings receiving I and IF (Fig. 2b). Slow-growing species perform better when resources are scarce because of their conservative use of resources (Reich et al. 2003; Reich 2014; Noulèkoun et al. 2017), which explains the differences observed in the response to the treatments by the fast-growing and slow-growing species during the dry season.

Of the five species, *L. leucocephala* produced the greatest total biomass (2.1 kg tree⁻¹) at 15 MaP on the degraded cropland, with the total biomass of manured *L. leucocephala*

Fig. 4 Fractional allocation to roots (RMF) relative to total sapling dry mass for *M. oleifera* (a), *J. curcas* (b), *L. leucocephala* (c), *A. occidentale* (d), *P. biglobosa* (e), and all species combined (f) in response to the control (C), fertilization (F), irrigation (I), and fertilization + irrigation (IF). Total dry mass values were natural log-transformed. Data from three harvests (5, 11, and 15 MaP) are considered



saplings almost doubling that of *M. oleifera* and *J. curcas* (Figs. 2c and 3c). This demonstrates the strong potential of this species in afforestation schemes. The leguminous *L. leucocephala*, known as a “fertilizer tree,” has been

recommended for the restoration of impoverished lands (Garrity et al. 2010). In addition, we found that manuring boosted the biomass production of *L. leucocephala*, possibly due to the increased supply of P, which enhances N₂

Table 2 Slope comparison for the relationship between the fractional allocation to roots (RMF) and total dry mass for five woody species under the control (C), fertilization (F), irrigation (I), and fertilization + irrigation (IF) treatments

Treatment	<i>M. oleifera</i>	<i>J. curcas</i>	<i>L. leucocephala</i>	<i>A. occidentale</i>	<i>P. biglobosa</i>
Control (C)	-0.093b	-0.041a	-0.024b	-0.006a	-0.091a
Fertilization (F)	-0.030a	-0.039a	-0.036b	-0.002a	-0.014a
Irrigation (I)	-0.099b	-0.049a	-0.056ab	-0.018a	-0.146a
Fertilization + irrigation (IF)	-0.065ab	-0.041a	-0.073a	-0.031a	-0.038a
Mean across treatments	-0.066B	-0.035B	-0.044B	-0.002A	-0.044B

Within columns and for treatments, values followed by the same lowercase letter are not significantly different. Within a row, species means followed by the same uppercase letter are not significantly different. For all the cases of equal slopes between the treatments, the comparison of the intercepts showed no significant difference (data not shown). A significance level of $P < 0.05$ was used for the LSD post hoc test

Table 3 Allometric coefficients (k) and coefficient of determination (R^2) for the root and shoot relationship of five woody species under the control (C), fertilization (F), irrigation (I), and fertilization + irrigation (IF) treatments

Treatments	<i>M. oleifera</i>	<i>J. curcas</i>	<i>L. leucocephala</i>	<i>A. occidentale</i>	<i>P. biglobosa</i>
Control (C)	0.564b	0.721a	0.855a	0.965a	0.593a
Fertilization (F)	0.814a	0.755a	0.803a	0.982a	0.821a
Irrigation (I)	0.561b	0.747a	0.764a	0.866a	0.428a
Fertilization + irrigation (IF)	0.674ab	0.793a	0.667a	0.741a	0.799a
Mean across treatments	0.658C	0.785B	0.777B	0.981A	0.751AB
R^2	0.836	0.812	0.918	0.942	0.851

Within columns and for treatments, values followed by the same lowercase letter are not significantly different. Within a row, species means followed by the same uppercase letter are not significantly different. For *J. curcas*, *L. leucocephala*, and *A. occidentale*, the comparison of intercepts between the treatments showed no significant difference. Intercepts were significantly different between the treatments for *P. biglobosa* (data not shown). A significance level of $P < 0.05$ was used for the LSD post hoc test

fixation in trees growing in P-poor agricultural soil (Djumaeva et al. 2013).

The limited response to irrigation during the dry season can be attributed to (i) a greater importance of nutrient over water stress under semi-arid conditions (Reubens et al. 2011; Noulèkoun et al. 2017), (ii) the relatively low amount of water supplied per plant during the dry season, and (iii) the deciduousness of the tree species as a drought-escaping mechanism inducing dormancy during dry periods (e.g., Monasterio and Sarmiento 1976; Reich and Borchert 1984; Poorter and Markesteijn 2008). In the fast-growing species, the deciduousness also caused a decrease in biomass accumulation between 5 and 11 MaP. However, the effect of supplemental irrigation may extend beyond the dry season period in which it was applied, as shown by the enhanced longitudinal and cambial growth of shoots and roots in same trial at 15 MaP (Noulèkoun et al. 2017), the extended photosynthetically active period in coppicing trees in South Africa (Moyo et al. 2015), and the overall rise in AGB production in a long-term afforestation trial in arid Uzbekistan (Khamzina et al. 2008). This post-irrigation

effect was particularly evident in the slow growers, which exhibited comparable total biomass production under the I, F, and IF treatments at 15 MaP (Fig. 2c).

4.2 Biomass allocation as influenced by ontogeny and resource availability

Previous studies aiming to understand the effects of increased resource availability on biomass allocation in deciduous species (Achten et al. 2010) and conifers (Coyle and Coleman 2005) have reported conflicting results, presumably because the impact of ontogeny was not always considered (McCarthy and Enquist 2007). In our study, except for *A. occidentale*, the RMF dropped for all species and across all treatments over time (Fig. 3 and $k < 1$, Table 3), confirming that the partitioning of biomass to belowground was predominantly controlled by ontogeny (Table 4). Similar ontogenetically induced falls in the RMF have been reported for seedlings (Coleman et al. 1998) and 3–4-year-old plantations of loblolly

Table 4 Multiple regression parameters according to tree species demonstrating the relative importance of ontogeny (total dry mass), fertilization, and irrigation for belowground biomass allocation. The dependent variable is root dry mass. A and B represent the intercept and slope of the robust linear regression

Species	Independent variable	A	B	Prob > F	Model R^2
<i>M. oleifera</i>	Total biomass	0.299	0.775	<0.001	0.861
	Fertilization	5.335	-0.089	0.458	0.007
	Irrigation	5.331	-0.143	0.336	0.014
<i>J. curcas</i>	Total biomass	-0.684	0.874	<0.001	0.855
	Irrigation	4.645	0.488	0.006	0.109
<i>L. leucocephala</i>	Total biomass	-0.278	0.849	<0.001	0.945
	Irrigation	5.027	0.242	0.242	0.019
<i>A. occidentale</i>	Total biomass	-1.903	0.991	<0.001	0.944
	Fertilization	3.347	0.097	0.656	0.003
	Irrigation	2.973	1.251	<0.001	0.427
<i>P. biglobosa</i>	Total biomass	-0.265	0.909	<0.001	0.951

Backward-stepwise selection was used to identify the most important independent variables. Multiple regression was then run to determine the relative variation explained by each. Data presented here are for the most important variables only

pine and cottonwood genotypes (Coyle and Coleman 2005; Coyle et al. 2008) in humid sub-tropical climates.

After accounting for ontogeny (by comparing k), our results revealed either that there was no impact by I and F on biomass partitioning (e.g., in *J. curcas* and *P. biglobosa*) or that there was a shift toward greater root biomass (i.e., greater k values) in nutrient-rich conditions (e.g., in *M. oleifera*). This indicates that resource availability has no consistent effect on BGB allocation in fast-growing and slow-growing species during early growth stages. The lack of consistent shifts in biomass allocation to belowground due to nutrient and water amendments, also evidenced by variations in the decrease in the RMF between treatments for *M. oleifera* and *L. leucocephala* (Table 2), has been reported earlier for grasses (McConnaughay and Coleman 1999; Reich 2002) and 3-year-old woody plants (Coyle and Coleman 2005). The evidence combined thus suggests that patterns in optimal biomass partitioning in relation to resource variation after controlling for size are variable and—to a large extent—unpredictable. According to OPT, a greater proportion of roots, the organs responsible for resource acquisition, is expected under low-nutrient or low-moisture conditions (McConnaughay and Coleman 1999). This pattern was observed in *M. oleifera* (Fig. 4a), but the opposite occurred in N₂-fixing *L. leucocephala* (Fig. 4c). Therefore, much of the variation in biomass partitioning explained by OPT is driven by differences in plant size and tree species rather than results from true plasticity in biomass allocation (McConnaughay and Coleman 1999; McCarthy and Enquist 2007).

The scaling slope (k) of the allometric relationship between AGB and BGB was close to 1.0 for *A. occidentale* (Table 3). This finding is consistent with the allometric scaling theory (Enquist and Niklas 2002; Niklas and Enquist 2002), given that the relationship between root and shoot biomass is isometric over the considered size range (40–1400 g). In contrast, the scaling exponents for the other species were lower, ranging between 0.66 and 0.78. This discrepancy between observation and theory could be due to the variation in biomass partitioning between aboveground and belowground as a consequence of species-specific adaptations to water-limited and nutrient-limited conditions (Enquist and Niklas 2002). It is also possible that there were systematic errors associated with excavating the entire rooting systems, leading to an underestimation of the root biomass (Robinson 2004) and thus reducing the numerical values of the scaling exponents (Niklas 2004).

4.3 Implications for the afforestation of degraded croplands

Trade-offs between rapid growth, resource utilization, and site adaptability arise when selecting suitable species for forest plantations (Aubrey et al. 2012). Fast-growing species are considered competitive but are narrow site adapted and require

adequate resources to optimize productivity. Slow growers are more stress-tolerant and thus suitable to a broad range of environments (Aubrey et al. 2012). Of the five tested species, planting fast-growing *M. oleifera*, *J. curcas*, and *L. leucocephala* with an adequate nutrient supply has the highest production potential, as evidenced by their greater biomass production and strong positive response to fertilization (Fig. 2). This could increase return rates for investment in afforestation, but only for a limited expanse of plantation acreage due to the narrow site requirements of these species. In contrast, the slow-growing *A. occidentale* and *P. biglobosa* achieved reasonable biomass production and exhibited a more plastic response to treatments, as evidenced by the large range of treatment-induced increase in biomass. Considering the vast area of degraded croplands in SSA, afforestation using slow growers may produce a larger volume of biomass over the landscape as a whole. Overall then, a mixed cultivation of fast-growing and slow-growing species (Khamzina et al. 2006; Noulèkoun et al. 2017) seems to be most suitable for sustaining land cover.

The productivity of the 2-year-old afforestation site (5.8 Mg ha⁻¹ year⁻¹) was about three times greater than that of the 10-year-old fallow (1.9 Mg ha⁻¹ year⁻¹). This comparative advantage of plantations over natural succession is due to both the silvicultural management in plantations and the slow regeneration and unsustainable grazing of fallow land.

5 Conclusion

Belowground biomass represented a substantial share (up to 77%) of the total biomass of afforestation species in the early growth stages. However, with increasing tree size, a greater proportion of biomass was allocated to aboveground. Ontogeny rather than resource availability was the main driver of the observed shift in biomass partitioning. This implies that biomass allocation in young multi-species plantations can be captured by simple allometric coefficients, thereby improving predictions of growth models for young forest stands. On the other hand, increased resource availability through silvicultural treatment accelerated sapling biomass production, which overall led to the greater production of AGB. Fast-growing tree species produced more biomass, responding more vigorously to silvicultural treatments during the rainy seasons than did the slow growers. Significant treatment-induced increases in biomass and the ability to adjust production in resource-limited conditions were the key characteristics of slow-growing species. For these reasons, we suggest the use of both fast-growing and slow-growing tree species in the afforestation of degraded croplands.

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Compliance with ethical standards

Data availability This manuscript has data included as electronic supplementary material. The datasets generated and/or analyzed during the current study are available from the first or corresponding author on reasonable request.

Conflict of interest The authors declare that they have no conflict of interest.

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Electronic supplementary materials for Noulèkoun et al. (2017b)

Biomass allocation in five semi-arid afforestation species is driven mainly by ontogeny rather than resource availability

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Appendix S1: Significance levels of the aggregate effects of treatments (control (C), fertilization (F), irrigation (I) and irrigation + fertilization (IF)) on five woody species (*M. oleifera*, *J. curcas*, *L. leucocephala*, *A. occidentale* and *P. biglobosa*) on a degraded cropland in northern Benin after the first growing season (0-5 MaP), the dry season (5-11 MaP) and the second growing season (11-15 MaP). P-values lower than $\alpha=0.05$ are indicated in bold

Time	Species	Shoot ^a	Root ^b	Total ^c
5 MaP	<i>M. oleifera</i>	0.004	0.805	0.042
	<i>J. curcas</i>	0.032	0.097	0.034
	<i>L. leucocephala</i>	0.032	0.079	0.033
	<i>A. occidentale</i>	0.393	0.893	0.470
	<i>P. biglobosa</i>	0.054	0.141	0.062
	Species mean across treatment	<0.001	<0.001	<0.001
11 MaP	<i>M. oleifera</i>	0.592	0.071	0.362
	<i>J. curcas</i>	0.189	0.809	0.405
	<i>L. leucocephala</i>	0.318	0.229	0.278
	<i>A. occidentale</i>	0.347	0.042	0.283
	<i>P. biglobosa</i>	<0.001	<0.001	<0.001
	Species mean across treatment	<0.001	<0.001	<0.001
15 MaP	<i>M. oleifera</i>	0.006	0.224	0.013
	<i>J. curcas</i>	<0.001	<0.001	<0.001
	<i>L. leucocephala</i>	<0.001	0.002	<0.001
	<i>A. occidentale</i>	0.001	0.005	0.001
	<i>P. biglobosa</i>	<0.001	<0.001	<0.001
	Species mean across treatment	<0.001	<0.001	<0.001

^a Shoot= Leaves + Stem; fruit biomass was not included in the analysis.


^b Root= Coarse roots + Fine roots

^c Total= Shoots + Roots

Appendix S2: Root mass fraction (RMF) statistics for five woody species at 5, 11 and 15 months after planting (MaP) on a degraded cropland in northern Benin. P-values lower than $\alpha = 0.05$ are indicated in bold

Factors	RMF
	5 MaP
Species (S)	<0.001
Fertilization (F)	<0.001
S x F	0.009
	11 MaP
Species (S)	<0.001
Fertilization (F)	0.006
S x F	0.001
Irrigation (I)	0.823
S x I	0.036
F x I	0.006
S x F x I	0.124
	15 MaP
Species (S)	<0.001
Fertilization (F)	<0.001
S x F	0.329
Irrigation (I)	0.072
S x I	0.188
F x I	0.572
S x F x I	0.525

Sapling biomass allometry and carbon content in five afforestation species on marginal farmland in semi-arid Benin

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Abstract Allometric equations are routinely used in the estimation of biomass stocks for carbon accounting within forest ecosystems. However, generic equations may not reflect the growth trajectories of afforestation species that are introduced to degraded farmland characterized by water and nutrient limitations. Using sequential measurements of the height, basal diameter, and above- and belowground biomass of juvenile trees, we developed allometric equations for five woody species (*Moringa oleifera* Lam., *Leucaena leucocephala* Lam., *Jatropha curcas* L., *Anacardium occidentale* L. and *Parkia biglobosa* Jacq.) subjected to a gradient of water and nutrient availability in an afforestation trial on degraded cropland in the semi-arid zone of Benin, West Africa. For three of the species studied, the allometric relationships between basal diameter and biomass components (i.e. leaves, stems and roots) were described best by a simple power-law model ($R^2 > 0.93$). The incorporation of species-specific height–diameter relationships and total height as additional predictors in the power-law function also produced reasonable estimates of biomass. Fifteen months after planting, roots accounted for 10–58% of the total biomass while the root-to-shoot ratio ranged between 0.16 and 0.73. The total biomass of the saplings ranged between 1.4 and 10.3 Mg ha⁻¹, yielding 0.6–4.3 Mg C ha⁻¹, far exceeding the biomass in the traditional fallow system. The rate of stem carbon sequestration measured ca. 0.62 Mg C ha⁻¹ year⁻¹. Overall, the allometric equations developed in this study are generally useful for assessing the standing shoot and root biomass of the

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five afforestation species during the juvenile growth stage and can help in reporting and verifying carbon stocks in young forests.

Keywords Carbon stock · Height–diameter allometry · *Jatropha curcas* · Power function · Roots · West Africa

Introduction

Deforestation and forest degradation, particularly in (sub-)tropical developing countries contribute substantially to carbon dioxide (CO₂) emissions into the atmosphere (Pearson et al. 2017). International programs (e.g. REDD + and CDM) have been set up to support national efforts towards carbon sequestration and combat desertification through afforestation and reforestation (AR) activities (UNFCCC 1997, 2010; Hosonuma et al. 2012). In this regard, afforestation using multi-purpose tree species has been widely promoted as a way to restore degraded drylands and improve rural livelihoods by providing bioenergy feedstock (Baumert et al. 2018) and marketable non-timber forest products, including carbon credits (Djanibekov et al. 2013; Yeboah et al. 2014).

Reporting and verifying the biomass and carbon dynamics of afforested areas for REDD + and recent efforts to increase the plantation acreage of commercially important tree species in West African drylands (e.g. <http://www.thp.org/the-miracle-moringa-tree>. Accessed 4/22/2017) need to be accompanied by accurate documentation of the growth potential of the tree species considered for afforestation. However, information about carbon concentration, growth allometry, and sapling survival is still lacking, meaning realistic projections for carbon sequestration using multi-species afforestation in semi-arid Africa are difficult to achieve (Yeboah et al. 2014; Weber et al. 2017; Baumert et al. 2018). Developing a database for this information and using it to derive allometric equations that can be used for tree growth predictions is the starting point for addressing the informational gap in Africa. The findings can be further incorporated into process-based models to extend the applicability of the results across a wide range of semi-arid environmental conditions (Kalliovirta and Tokola 2005; Blujdea et al. 2012).

Very few allometric models are available for use in predicting the standing biomass of tree species in sub-Saharan Africa (e.g. Henry et al. 2011; Baumert and Khamzina 2015; Tjeuw et al. 2015), and of those, the majority were derived using data from mature trees (Nelson et al. 2014), which exhibit relatively little variability in biomass. Moreover, trees introduced on marginal land, which is characterized by poor soils, often differ in terms of growth trajectory from those growing in more favourable edaphic conditions or under more intensive management (Delagrange et al. 2004; Lupi et al. 2017; Noulèkoun et al. 2017a). Hence, the lack of biomass data for juvenile forests and tree plantations under sub-optimal soil conditions results in inaccurate estimates of biomass and carbon stocks, affecting carbon accounting and management decisions (Blujdea et al. 2012).

The robustness of allometric predictions depends on the model's choice and its adequacy to capture prevalent growing conditions (Chave et al. 2004; Sileshi 2014; Picard et al. 2015). The power-law equation is the most commonly used allometric model for estimating biomass based on stem diameter or height or their combination (e.g. Brown 1997; Sileshi 2014; Baumert and Khamzina 2015). The inclusion of height in allometric models has reportedly led to little or no improvement in the performance of these models, suggesting that stem diameter (i.e. the diameter at breast height, DBH or basal diameter, *D*) alone is a robust predictor of aboveground biomass (AGB; Youkhana and Idol 2011;

Kuyah et al. 2012a, 2013, 2016; Lin et al. 2017; Paul et al. 2016) and belowground biomass (BGB) (Kuyah et al. 2012b; Baumert and Khamzina 2015) for mature plants of various tree species and irrespective of the land-use systems observed in both humid and (semi)-arid tropics. Whether the addition of height as a predictor would yield less biased biomass estimates for young trees in afforestation systems has yet to be analysed.

Site characteristics (i.e. climate and soil properties), tree morphology and ontogenetic stages reportedly influence biomass growth and hence the accuracy of biomass prediction (e.g. Ketterings et al. 2001; Chave et al. 2004; Pilli et al. 2006; Chave et al. 2014; Baumert and Khamzina 2015). Given the uncertainty in allometric equations induced by the variation of model parameters between sites, Ketterings et al. (2001) suggested the incorporation of site-specific height–diameter relations into the power model. Therefore, when generalizing allometric predictors to enhance their scope and extend their applicability to a wide range of forest systems, the degree of local specificity and allometric model's suitability still needs to be taken into account.

Allometric equations for predicting BGB, a considerable biotic carbon pool, are less commonly reported than those for AGB due to the methodological challenges associated with root excavation (Mokany et al. 2006; Baumert and Khamzina 2015). Therefore, the BGB is often estimated using the root: shoot ratio (RSR) assuming that the RSR reflects the differential investment of resources between above- and belowground organs under the influence of biotic, abiotic and management factors (Mokany et al. 2006). Broad-scale derived RSRs, e.g. IPCC default value, have been widely used to quantify BGB for carbon accounting in the absence of locally valid RSRs (IPCC 2003; Mokany et al. 2006). Since the information is largely unavailable for many dryland afforestation species, the development of allometric equations and RSR is necessary for a reliable estimation of BGB.

This study thus aimed to (1) develop allometric equations to estimate the standing biomass (i.e. the leaves, stems and roots) of juvenile trees of five drought-deciduous woody species proposed for the afforestation of degraded lands in the semi-arid zone of Northern Benin and similar agro-ecological conditions in West Africa, and (2) validate the elaborated equations with independent datasets and against the available allometric equations for tropical semi-arid tree plantations and forests. Based on empirical data for the biomass and carbon concentration in plant tissues, the carbon stocks and partitioning between the above- and belowground biomass of saplings were quantified for a multi-species afforestation system on degraded cropland.

Materials and methods

Study area

A multi-species afforestation experiment was established on degraded cropland in July 2014 in Pouri village (N10°54'8.4" and E1°4'47.4"), located in the semi-arid Atacora Department of Northern Benin (Fig. 1, Noulèkoun et al. 2017a). The climate in the study area is characterized by a single rainy season (April–October) followed by a dry season (November–March). The long-term (1986–2015) annual precipitation averages about 1085 mm while temperatures range between 11 and 45 °C, with an annual mean of 27.5 °C.

The experimental afforestation site was savanna forest prior to being clear cut and next cropped with a successional 3-year intercrop of either sorghum and cowpea or maize

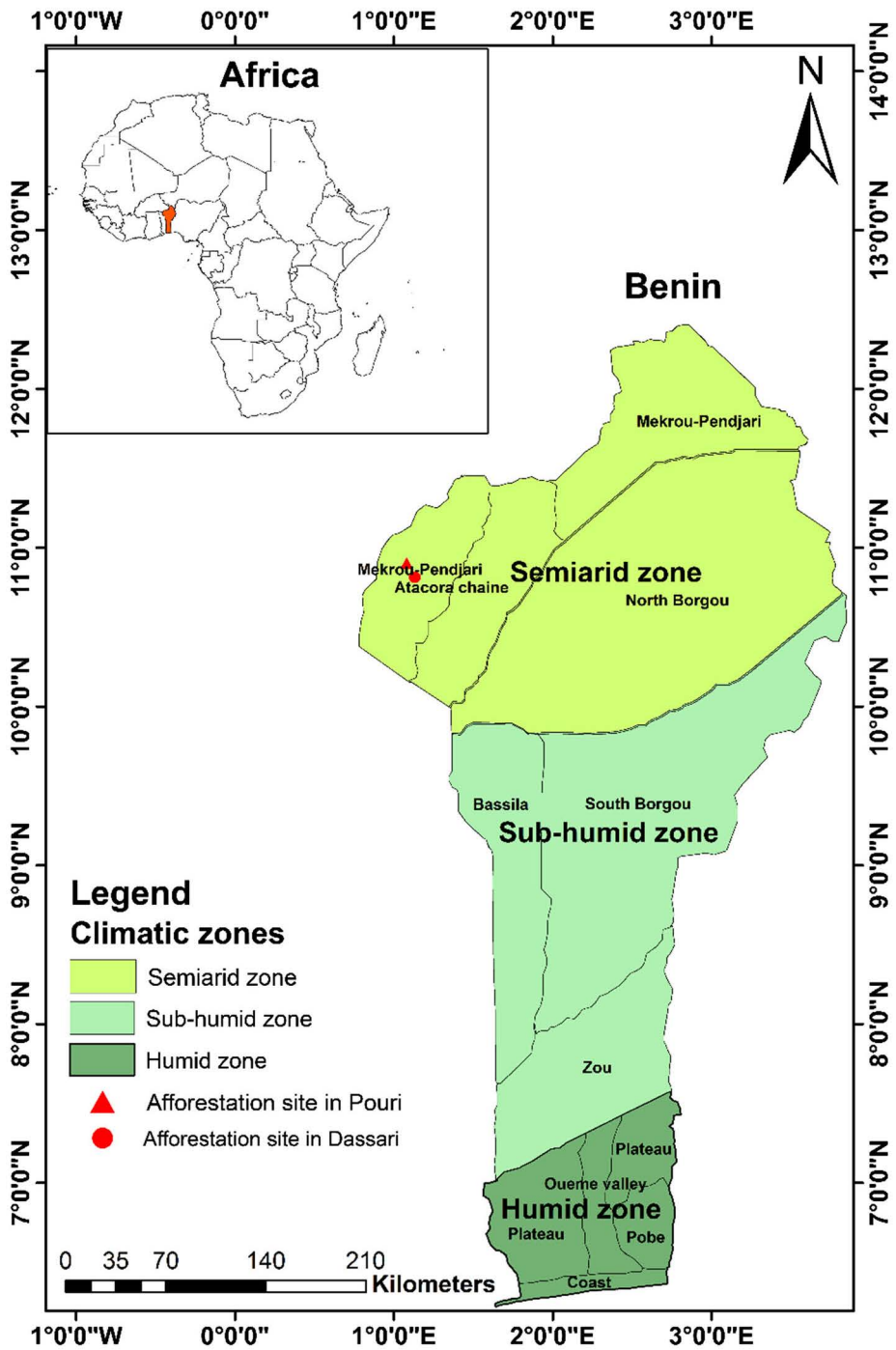


Fig. 1 Location of the afforestation sites in the semi-arid climate zone of Northern Benin

followed by yam for about a decade. The site experienced a decline in crop yields and soil nutrients prior to afforestation. More site details have been reported previously (Noulèkoun et al. 2017a).

Plant material and experimental design

Five (semi-) deciduous tree and shrub species of socio-economic importance in the study region were included in the experiment (Table 1). All five species provide food and/or medicine for human consumption and ecosystem services of relevance to land reclamation. Plantation establishment consisted of mechanical soil preparation (i.e. the clearing of sparse woody vegetation, ploughing and fencing) and manual transplantation of seedlings after 2.5–4 months following germination at a local nursery 15–20 km from the experimental site. All seedlings were raised from seeds collected from mature trees growing in the study area. The number of sampled trees ranged from at least 2 for *L. leucocephala* and *P. biglobosa* to 4 or 5 for the other species (personal communication with the tree nursery supervisor).

The experiment compared plant growth between untreated control plots (i.e. no silvicultural treatments) and plots subject to manuring, irrigation or combinations of both (Noulèkoun et al. 2017a). The initial stand density was 5000 trees ha⁻¹ (2 × 1 m spacing).

Table 1 General characteristics and stem dimensions (basal diameter [cm] and height [m]) of the sampled saplings for five afforestation species in the semi-arid region of Northern Benin

Tree species (common name)	Growth form	Number of trees	Mean (min, max)		Products, services, and uses ^a
			Diameter	Height	
<i>Moringa oleifera</i> Lam. (Drumstick tree)	Small tree	84	5.1 (2.6, 8.3)	2.8 (1.2, 4.4)	Food, fodder, firewood, medicine, soil fertility improvement, erosion control, live fences and windbreaks
<i>Jatropha curcas</i> L. (Physic nut)	Shrub or small tree	84	5.1 (2.8, 7.7)	1.2 (0.8, 1.8)	Bioenergy, medicine, soil fertility improvement, erosion control, live fences, afforestation of marginal land
<i>Leucaena leucocephala</i> Lam. (Leucaena)	Small or medium-sized tree	84	3.2 (1.6, 7.3)	2.2 (1.1, 3.9)	Food, fodder, firewood, nitrogen fixation, soil fertility improvement, erosion control, windbreaks and intercropping
<i>Anacardium occidentale</i> L. (Cashew)	Medium-sized tree	72	2.6 (1.2, 5.2)	0.9 (0.4, 1.9)	Food, fodder, firewood, intercropping
<i>Parkia biglobosa</i> Jacq. (African locust bean)	Tree	57	1.4 (0.4, 3.9)	0.5 (0.2, 1.4)	Food, fodder, firewood, timber, soil fertility improvement, windbreaks and intercropping

^aDerived from Orwa et al. (2009). Only products and services specific to Northern Benin are indicated

Measurements, biomass sampling and carbon content analysis

Juvenile tree growth was monitored during the first 15 months after planting (MaP) covering the rainy seasons of 2014 and 2015 and the intervening dry season. Just before planting the seedlings in the field (i.e. MaP = 0), ten plants of each species were randomly chosen to determine the mean reference values for different biomass components. Next, biometric measurements were conducted at 5 MaP (corresponding to the end of the 2014 rainy season), 11 MaP (the end of the 2015 dry season) and 15 MaP (the end of the 2015 rainy season). Height (H , m) and the basal diameter (D , cm) were measured for 2–6 randomly selected juvenile trees per experimental plot (Noulèkoun et al. 2017a). Subsequently, the measured trees were felled and the aboveground parts separated into leaves (including the petiole), stems, branches, and (if present) reproductive parts. Next, the entire rooting system was manually excavated, washed free of soil on a sieve and sectioned into coarse ($\phi > 2$ mm) and fine ($\phi < 2$ mm) fractions. The fresh mass of all harvested fractions was recorded in the field using a 7-kg portable scale (accuracy 0.1 g). Sub-samples of the harvested fractions were oven-dried at 75 °C until constant weight and their dry mass determined. Woody fractions were cut into small pieces to facilitate the drying process. The oven-dried sub-samples collected at 15 MaP were finely ground and analysed for carbon concentration using a mass spectrometer (ANCA-SL/20-20, SerCon, UK), with 2 replicates per sample.

Allometric analyses

The conventional power-law equation ($Y = \alpha X^\beta$) was used to describe the empirical allometric relationship between tree biological traits Y and X . To avoid challenges associated with ordinary least squares (OLS) log-linear regression and back-transformation of the log-transformed equation into its initial form (Packard et al. 2011; Sileshi 2014; Kuyah et al. 2016), a nonlinear regression was fitted to the power-law equations (Eqs. 1, 2, 3, 4). The robust standard error estimation option in STATA was used to control for heteroscedasticity (StataCorp 2015). In this analysis, 95% confidence intervals (CIs) and the percent relative standard error (PRSE), i.e. the standard error (SE) of the parameter divided by its absolute value (Sileshi 2014), were used to reflect uncertainty in the model's estimates of the scaling coefficient (α) and the exponent (β). A parameter estimate was considered unreliable if its PRSE was $> 30\%$ (Sileshi 2014). Data from all three harvest periods and treatments were pooled for the analyses to increase the generalizability of the equations for the large range of tree diameters (Table 1) found in saplings under various nutrient and water availability gradients (the effect of age and treatment on the allometric relationships is presented in Appendix 1, Supplementary Material). Reproductive biomass (i.e. the fruit of *J. curcas* and pods of *M. oleifera*) was omitted from the analyses as suggested by Niklas and Enquist (2002) because it represented only a minor proportion (2–5%) of the total biomass. Only coarse roots were considered in the estimation of root carbon stocks.

Relationship between height (H) and diameter (D)

Since allometric relations are influenced by growth stages (Pilli et al. 2006), the relationship between tree height and diameter (H – D) was initially analysed by plotting H (m) versus D (cm) to identify the ontogenetic stages of each species. Next, the H – D growing

functions were described by fitting either a linear or quadratic curve (Sit 1994; Pilli et al. 2006). The power function was further applied to establish the empirical allometric relationships between H and D according to:

$$H = kD^c, \quad (1)$$

where c represents the estimate of the site-specific H – D relationship (Ketterings et al. 2001).

Relationship between biomass (M) and diameter (D)

An allometric power model with D as the sole predictor variable (Eq. 2), an allometric power model with D in combination with H (Eq. 3), and the model suggested by Ketterings et al. (2001; Eq. 4), which incorporates the site-specific H – D relationship (c , Eq. 1), were all tested for their ability to predict biomass:

$$M = \alpha D^\beta \quad (2)$$

$$M = \alpha (D \times H)^\beta \quad (3)$$

$$M = \alpha D^{2+c}. \quad (4)$$

For each species, the allometric relationship between each biomass fraction (i.e. leaves, stems, and roots) and D was analysed according to Eqs. (2), (3) and (4). The selection of the best fitting equation was based on the highest coefficient of determination (R^2), the lowest root mean square of error (RMSE), the lowest mean absolute percentage error (MAPE), and the lowest mean relative error (MRE) between the predicted (M_p) and corresponding observed (M_o) biomass values:

$$MAPE = \frac{100}{n} \sum_{i=1}^n \frac{|M_p - M_o|}{M_o} \quad (5)$$

$$MRE = \frac{100}{n} \sum_{i=1}^n \frac{M_p - M_o}{M_o}. \quad (6)$$

Model validation

The available independent dataset (Baumert and Khamzina 2015) was used to validate the equations developed for *J. curcas*. The dataset ($n = 101$) contained observations of the woody AGB (WAGB), BGB and D (0.7–20 cm) of *J. curcas* trees grown in various cultivation systems including small-scale intercropping, marginal land afforestation, intensively managed plantations, live fences and contour hedges in the semi-arid zones of Burkina Faso. An additional validation dataset was derived from an afforestation trial in Dassari village in Benin, located 8–10 km from the experimental site (Fig. 1). This dataset included WAGB and BGB observations of 78 saplings ($1.5 < D < 7.3$ cm). At Dassari village, the seedlings were planted in July 2014 on agricultural fallow land and subjected to the same silvicultural treatments as in Pouri.

The scatter plot of predicted versus observed values and the test of significance of slope ($b = 1$) and intercept ($a = 0$) were used for evaluating the quality of model fit (Piñeiro et al. 2008; Sileshi 2014). The predicted biomass values were simulated by Eq. (2).

Statistical analyses

All statistical analyses were performed using STATA 14 (StataCorp 2015). The normality and homoscedasticity of the errors were checked using: (1) a skewness and kurtosis test, (2) normal and kernel density distributions and (3) a plot of residuals against fitted values. A linear mixed-effect model with the least significant difference (LSD) post hoc test for mean separation was used to assess differences in MAPE with respect to the equations (Eqs. 2, 3, 4) and biomass fractions. The random term in the model was plot identity, while the fixed terms included the equations and biomass fractions.

Results

Relationship between tree H and D

An analysis of the H and D ratio in order to identify potentially different growth stages revealed a linear pattern for all species except *M. oleifera*. Although there was a square misspecification according to the link test ($_hatsq < 0.05$) for the latter species, the point of inflection fell outside the data range. Consequently, for all five species, only one growth phase (juvenile) was recognised for the subsequent analyses.

Significant and strong allometric relationships ($p < 0.0001$; Table 2) were observed between H and D for all the species with reliable parameter (k and c) estimates (PRSE $< 11\%$). No obvious pattern was detectable in the scatter plots of the residuals.

Table 2 Estimates of allometric parameters (k and c), percent relative standard error (PRSE) and coefficient of determination (R^2) for the relation between height (H , m) and basal diameter (D , cm) using Eq. (1) ($H = kD^c$) for five afforestation species

Species	N	k (PRSE)	95% CI for k	c (PRSE)	95% CI for c	R^2
<i>M. oleifera</i>	84	0.71 (9.1)	0.58–0.84	0.85 (6.2)	0.74–0.95	0.98
<i>J. curcas</i>	84	0.48 (7.7)	0.41–0.56	0.57 (8.4)	0.47–0.66	0.99
<i>L. leucocephala</i>	84	0.88 (6.6)	0.76–0.99	0.79 (7.7)	0.67–0.91	0.98
<i>A. occidentale</i>	72	0.49 (5.3)	0.44–0.54	0.76 (7.2)	0.65–0.87	0.98
<i>P. biglobosa</i>	57	0.37 (4.4)	0.34–0.40	0.83 (10.6)	0.66–1.01	0.93

Reported are the number of trees (N) and the confidence interval (CI) of each estimate

k is the scaling coefficient of the allometric relationship between H and D ; c represents both the scaling exponent and the estimate of the site-specific H – D relation

Allometric equations

Aboveground biomass

The empirical allometric coefficients for estimating the biomass of each aboveground fraction using the different equations are presented in Table 3. All models had significant ($p < 0.0001$) and reliable parameter estimations (i.e. the estimates were within a 95% CI). Irrespective of the bio-fraction, higher R^2 and lower RMSE, MAPE and MRE values were observed for the model fitted to the power equation (Eq. 2) than for the power models incorporating H (Eq. 3) and the H - D relationship (Eq. 4) for *M. oleifera*, *J. curcas* and *A. occidentale* (Table 3). Incorporating the H - D relationship (Eq. 4) yielded a predictive power similar to that of the power model (Eq. 2) for *J. curcas* and *A. occidentale*. Adding H (Eq. 3) increased the predictive power by 2–23% for *P. biglobosa* and *L. leucocephala*, albeit with unreliable α estimates for the latter species, as evidenced by a PRSE $> 30\%$ for TAGB and LB. The comparison of model performance based on the MAPE and MRE between observed and estimated AGB revealed that incorporating the H - D relationship (Eq. 4) for *L. leucocephala* substantially reduced the prediction error by 17–20% compared to Eq. (3), although it resulted in a lower R^2 (Table 3).

Fitting the equations to leaf biomass (LB) resulted in lower predictive power compared to TAGB and WAGB for *M. oleifera*, *L. leucocephala* and *A. occidentale*. In particular, LB estimations were substantially biased for *P. biglobosa*. All models using WAGB as the dependent variable performed better than those using TAGB for *M. oleifera*, *J. curcas*, *L. leucocephala* and *P. biglobosa*, as evidenced by the increased R^2 (1–7%) and/or reduced MAPE and MRE (Table 3).

Belowground biomass

Similar to the models for AGB, all parameters considered as proxies for BGB were estimated with acceptable errors (PRSE $< 30\%$; Table 4). The power-law equation (Eq. 2) turned out to be the most precise and unbiased (i.e. highest R^2 and lowest RMSE, MAPE and MRE) in the prediction of the BGB of *M. oleifera*, *J. curcas* and *A. occidentale*. The model that included H (Eq. 3) performed better than the other models (Eq. 2 and 4) for *P. biglobosa*, whereas the power model incorporating the H - D relationship (Eq. 4) best described the BGB-basal diameter relationship for *L. leucocephala* (Table 4).

J. curcas equations validation

The scatter plots for the observed versus predicted WAGB and BGB values revealed no significant prediction errors for the “juvenile” ($D < 5.5$) and “afforestation” ($1.8 < D < 5.7$) datasets of Baumert and Khamzina (2015) or for the Dassari dataset. This was supported by the statistical test using $a = 0$ and $b = 1$, which revealed no significant departure ($p > 0.05$) of the fitted lines from the 1:1 lines (Fig. 2).

Biomass and carbon stocks

At the onset of the experimentation (MaP = 0), the mean (\pm standard error of the mean, SEM) stem biomass was 0.003 ± 0.001 Mg ha⁻¹ for *M. oleifera*, 0.010 ± 0.002 Mg ha⁻¹ for *J. curcas*, 0.002 ± 0.000 Mg ha⁻¹ for *L. leucocephala*, 0.009 ± 0.001 Mg ha⁻¹ for *A.*

Table 3 Model parameter estimates (α and β), percent relative standard error (PRSE) and goodness of fit statistics (coefficient of determination R^2 , root mean square error [RMSE], mean absolute percentage error [MAPE] and the mean relative error [MRE]) of the allometric relationships between total aboveground biomass (TAGB, kg tree⁻¹), woody aboveground biomass (WAGB, kg tree⁻¹) and leaf biomass (LB, kg tree⁻¹), and basal diameter (D , cm) for five afforestation species

Species	Biomass variables	Equations	Eq.	N	α (PRSE)	β (PRSE)	R^2	RMSE	MAPE (%)	MRE (%)
<i>M. oleifera</i>	TAGB	$M = \alpha D^\beta$	2	84	0.010 (25.2)	2.36 (6.2)	0.97	0.12	22.8 ^c	10.2
		$M = \alpha (D \times H)^\beta$	3	84	0.018 (17.3)	1.24 (4.5)	0.96	0.13	31.5 ^d	11.6
		$M = \alpha D^{2+c}$	4	84	0.004 (3.9)	2.85	0.96	0.13	19.1 ^{ab}	- 6.1
	WAGB	$M = \alpha D^\beta$	2	84	0.008 (22.4)	2.38 (5.4)	0.97	0.07	18.4 ^a	7.2
		$M = \alpha (D \times H)^\beta$	3	84	0.014 (14.1)	1.26 (3.6)	0.97	0.09	23.2 ^{bc}	7.1
		$M = \alpha D^{2+c}$	4	84	0.003 (3.7)	2.85	0.96	0.10	19.1 ^{ab}	- 7.6
	LB	$M = \alpha D^\beta$	2	60	0.010 (34.8)	1.49 (14.2)	0.93	0.04	19.9 ^{abc}	6.5
		$M = \alpha (D \times H)^\beta$	3	60	0.018 (21.9)	0.71 (12.2)	0.92	0.04	20.9 ^{abc}	6.5
		$M = \alpha D^{2+c}$	4	60	0.001 (7.6)	2.85	0.86	0.05	38.5 ^d	- 20.0
<i>J. curcas</i>	TAGB	$M = \alpha D^\beta$	2	84	0.004 (23.8)	2.93 (4.4)	0.96	0.13	32.2 ^c	10.7
		$M = \alpha (D \times H)^\beta$	3	84	0.024 (23.9)	1.64 (7.1)	0.93	0.18	39.9 ^f	18.3
		$M = \alpha D^{2+c}$	4	84	0.008 (2.8)	2.57	0.96	0.14	37.3 ^f	22.6
	WAGB	$M = \alpha D^\beta$	2	84	0.004 (21.2)	2.74 (4.4)	0.96	0.08	20.3 ^a	3.4
		$M = \alpha (D \times H)^\beta$	3	84	0.020 (24.2)	1.53 (8.2)	0.93	0.11	26.9 ^d	9.8
		$M = \alpha D^{2+c}$	4	84	0.005 (3.1)	2.57	0.96	0.08	21.7 ^{bc}	8.3
	LB	$M = \alpha D^\beta$	2	60	0.003 (24.3)	2.48 (5.3)	0.96	0.05	20.8 ^{ab}	4.4
		$M = \alpha (D \times H)^\beta$	3	60	0.015 (18.5)	1.40 (6.2)	0.95	0.06	25.3 ^{cd}	8.2
		$M = \alpha D^{2+c}$	4	60	0.003 (3.1)	2.57	0.96	0.05	20.5 ^{abc}	2.4

Table 3 continued

Species	Biomass variables	Equations	Eq.	N	α (PRSE)	β (PRSE)	R ²	RMSE	MAPE (%)	MRE (%)
<i>L. leucocephala</i>	TAGB	$M = \alpha D^\beta$	2	84	0.060 (36.5)	2.02 (13.7)	0.83	0.38	73.9 ^c	60.3
		$M = \alpha (D \times H)^\beta$	3	84	0.059 (32.3)	1.19 (11.8)	0.87	0.34	56.9 ^d	47.2
		$M = \alpha D^{2+c}$	4	84	0.016 (17.7)	2.79	0.77	0.44	31.1 ^b	1.2
	WAGB	$M = \alpha D^\beta$	2	84	0.036 (30.9)	2.06 (11.5)	0.88	0.21	57.9 ^d	46.2
		$M = \alpha (D \times H)^\beta$	3	84	0.035 (27.2)	1.21 (9.8)	0.90	0.19	42.8 ^c	34.2
		$M = \alpha D^{2+c}$	4	84	0.011 (15.8)	2.79	0.82	0.25	25.7 ^a	- 4.4
	LB	$M = \alpha D^\beta$	2	60	0.043 (42.6)	1.63 (19.8)	0.79	0.19	69.7 ^c	54.2
		$M = \alpha (D \times H)^\beta$	3	60	0.041 (37.6)	0.97 (16.9)	0.82	0.18	57.3 ^d	43.9
		$M = \alpha D^{2+c}$	4	60	0.006 (22.9)	2.79	0.67	0.24	34.1 ^{bc}	- 17.6
<i>A. occidentale</i>	TAGB	$M = \alpha D^\beta$	2	72	0.018 (11.5)	2.58 (2.9)	0.97	0.07	20.9 ^a	4.2
		$M = \alpha (D \times H)^\beta$	3	72	0.057 (13.1)	1.40 (6.4)	0.96	0.08	22.2 ^a	6.3
		$M = \alpha D^{2+c}$	4	72	0.014 (2.9)	2.76	0.97	0.07	20.5 ^a	- 5.2
	WAGB	$M = \alpha D^\beta$	2	72	0.008 (14.2)	2.69 (3.7)	0.97	0.04	23.3 ^a	6.8
		$M = \alpha (D \times H)^\beta$	3	72	0.026 (8.4)	1.46 (4.4)	0.95	0.04	22.9 ^a	8.9
		$M = \alpha D^{2+c}$	4	72	0.007 (3.5)	2.76	0.97	0.04	22.1 ^a	3.0
	LB	$M = \alpha D^\beta$	2	52	0.015 (20.0)	2.25 (6.6)	0.95	0.05	24.9 ^a	12.0
		$M = \alpha (D \times H)^\beta$	3	52	0.039 (20.0)	1.22 (11.0)	0.94	0.06	25.7 ^a	13.9
		$M = \alpha D^{2+c}$	4	52	0.007 (6.3)	2.76	0.94	0.06	27.9 ^a	- 15.7

Table 3 continued

Species	Biomass variables	Equations	Eq.	N	α (PRSE)	β (PRSE)	R ²	RMSE	MAPE (%)	MRE (%)
<i>P. biglobosa</i>	TAGB	$M = \alpha D^\beta$	2	57	0.025 (24.7)	2.00 (15.1)	0.84	0.04	60.8 ^d	39.4
		$M = \alpha (D \times H)^\beta$	3	57	0.070 (8.3)	1.15 (7.2)	0.94	0.03	38.2 ^{bc}	18.0
		$M = \alpha D^{2+c}$	4	57	0.010 (20.2)	2.83	0.78	0.05	51.5 ^c	- 27.9
	WAGB	$M = \alpha D^\beta$	2	57	0.010 (28.2)	2.01 (18.6)	0.84	0.02	57.0 ^d	46.1
		$M = \alpha (D \times H)^\beta$	3	57	0.028 (6.2)	1.20 (8.3)	0.96	0.01	26.9 ^a	16.4
		$M = \alpha D^{2+c}$	4	57	0.004 (23.0)	2.83	0.78	0.02	43.6 ^{bd}	- 27.1
	LB	$M = \alpha D^\beta$	2	40	0.023 (19.7)	1.69 (14.5)	0.90	0.02	113.2 ^{abcd}	100.8
		$M = \alpha (D \times H)^\beta$	3	40	0.052 (9.2)	0.96 (8.2)	0.92	0.02	89.5 ^{abcd}	76.2
		$M = \alpha D^{2+c}$	4	40	0.006 (22.0)	2.83	0.79	0.03	54.4 ^{bcd}	- 38.9

N is the number of trees (sample size) used to construct the models. For the leaf biomass (LB), data collected at the end of the dry season (i.e. 11 MaP) were excluded
 α and β are scaling coefficient and exponent, respectively

^aWithin each species, MAPE values followed by the same superscript letter are not significantly different according to LSD post hoc tests. A significance level of $p < 0.05$ was used as the threshold value

Table 4 Model parameter estimates (α and β), percent relative standard error (PRSE) and goodness of fit statistics (coefficient of determination R^2 , root mean square error [RMSE], mean absolute percentage error [MAPE] and the mean relative error [MRE]) of the allometric relationships between belowground biomass (BGB, kg tree^{-1}) and basal diameter (D , cm) for five afforestation species

Species	Equations	Eq.	N	α (PRSE)	β (PRSE)	R^2	RMSE	MAPE (%)	MRE (%)
<i>M. oleifera</i>	$M = \alpha D^\beta$	2	84	0.032 (28.2)	1.19 (9.9)	0.94	0.06	33.9 ^a	17.1
	$M = \alpha (D \times H)^\beta$	3	84	0.050 (18.3)	0.57 (10.9)	0.92	0.07	39.9 ^b	20.3
	$M = \alpha D^{2+c}$	4	84	0.001 (6.8)	2.85	0.80	0.11	40.8 ^{ab}	- 26.3
<i>J. curcas</i>	$M = \alpha D^\beta$	2	84	0.001 (17.3)	2.95 (3.4)	0.97	0.03	14.7 ^a	1.3
	$M = \alpha (D \times H)^\beta$	3	84	0.007 (15.0)	1.68 (4.7)	0.95	0.04	17.9 ^b	6.6
	$M = \alpha D^{2+c}$	4	84	0.002 (3.0)	2.57	0.97	0.03	19.3 ^b	12.5
<i>L. leucocephala</i>	$M = \alpha D^\beta$	2	77	0.024 (24.7)	1.87 (10.2)	0.90	0.09	43.0 ^b	30.9
	$M = \alpha (D \times H)^\beta$	3	77	0.027 (19.6)	1.06 (7.9)	0.91	0.09	35.3 ^a	24.7
	$M = \alpha D^{2+c}$	4	84	0.005 (15.8)	2.79	0.81	0.13	33.2 ^{ab}	- 20.9
<i>A. occidentale</i>	$M = \alpha D^\beta$	2	66	0.004 (19.1)	2.37 (6.5)	0.94	0.02	29.0 ^a	13.35
	$M = \alpha (D \times H)^\beta$	3	66	0.010 (10.3)	1.36 (4.1)	0.95	0.01	30.0 ^a	10.5
	$M = \alpha D^{2+c}$	4	72	0.002 (5.6)	2.76	0.94	0.02	25.6 ^a	- 7.5
<i>P. biglobosa</i>	$M = \alpha D^\beta$	2	54	0.032 (16.8)	1.43 (19.9)	0.88	0.03	53.8 ^a	38.3
	$M = \alpha (D \times H)^\beta$	3	54	0.070 (6.2)	0.75 (12.9)	0.89	0.03	54.9 ^a	38.1
	$M = \alpha D^{2+c}$	4	57	0.007 (27.3)	2.83	0.70	0.04	60.4 ^a	- 53.5

N is the number of trees (sample size) used to construct the models

α and β are scaling coefficient and exponent, respectively

^aWithin each species, MAPE values followed by the same superscript letter are not significantly different according to LSD post hoc tests. A significance level of $p < 0.05$ was used as the threshold value

occidentale and $0.002 \pm 0.000 \text{ Mg ha}^{-1}$ for *P. biglobosa*. At 15 MaP, TAGB was $5.2 \pm 0.3 \text{ Mg ha}^{-1}$ for *M. oleifera*, $5.3 \pm 0.3 \text{ Mg ha}^{-1}$ for *J. curcas*, $7.8 \pm 0.6 \text{ Mg ha}^{-1}$ for *L. leucocephala*, $3.2 \pm 0.3 \text{ Mg ha}^{-1}$ for *A. occidentale* and $0.8 \pm 0.1 \text{ Mg ha}^{-1}$ for *P. biglobosa*, with RSR of 0.32 ± 0.08 , 0.30 ± 0.06 , 0.34 ± 0.08 , 0.16 ± 0.04 and 0.73 ± 0.24 , respectively. Total biomass production differed significantly between the species ($p < 0.001$) with the highest total biomass accumulated at 15 MaP by *L. leucocephala* (10.3 Mg ha^{-1}), and the lowest by *P. biglobosa* (1.4 Mg ha^{-1} ; Supplementary Material, Appendix 2).

A comparison of the carbon concentration between the biomass fractions and species found that it varied between 40.3 and 43.8% (Supplementary Material, Appendix 2). Using the empirical carbon concentration data, the total carbon stock amounted to $0.6 \pm 0.002 \text{ Mg ha}^{-1}$ for *P. biglobosa*, $1.5 \pm 0.002 \text{ Mg ha}^{-1}$ for *A. occidentale*,

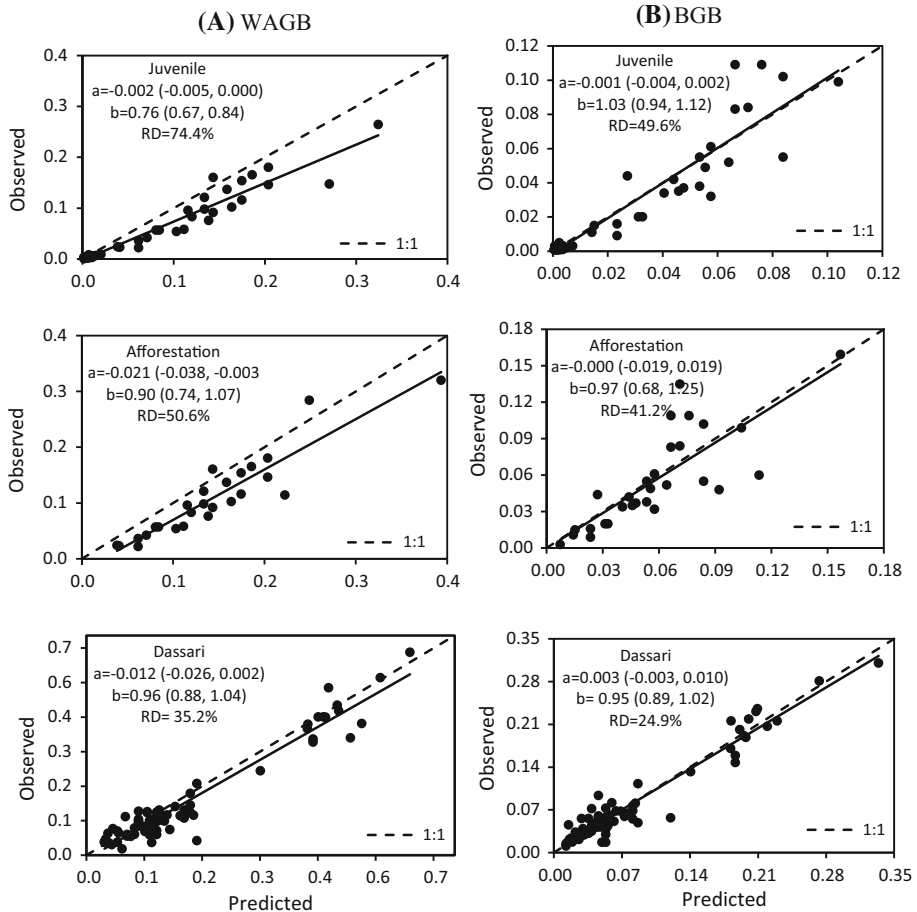


Fig. 2 Scatterplots of observed and predicted woody aboveground biomass (WAGB, A) and belowground biomass (BGB, B) derived from fitting *J. curcas* Eq. (2) to the Baumert and Khamzina (2015) data on juvenile trees (named as “Juvenile”) and trees grown in afforestation systems in Burkina Faso (“Afforestation”), and to the data of juvenile trees grown in the afforestation system in Dassari, Northern Benin (“Dassari”). Circles represent observed values, solid lines are fitted lines of the predicted values and dashed lines are the 1:1 lines. Test of significance of the intercept (a) and slope (b) is indicated by the 95% confidence intervals (values in parenthesis). If the 95% confidence interval of “a” covers 0 and that of “b” covers 1, then $a = 0$ and $b = 1$ cannot be rejected. The mean absolute percentage error (MAPE) and the mean relative error (MRE) between predicted and observed values are displayed

$2.8 \pm 0.003 \text{ Mg ha}^{-1}$ for *M. oleifera*, $2.8 \pm 0.003 \text{ Mg ha}^{-1}$ for *J. curcas*, and $4.3 \pm 0.007 \text{ Mg ha}^{-1}$ for *L. leucocephala*. The foliar carbon constituents were on average 18–61% of the AGB of these deciduous species. Furthermore, the carbon concentration in stems ranged between 40.3 and 42.8% in a comparison of the five species (Supplementary Material, Appendix 2). Assuming constant stem carbon concentration over the study period, the increase in stem carbon storage ranged from $0.10 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for *P. biglobosa* to $1.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for *M. oleifera*.

Considering all species together, the BGB accounted for about a quarter (24.7%) of total plant biomass ($6.21 \pm 0.43 \text{ Mg ha}^{-1}$), resulting in a mean and median RSR of

0.35 ± 0.03 and 0.31 , respectively. Based on the weighted average of the carbon content in the total biomass (41.7%) and the mean stem carbon concentration (41.5%) across all species, the saplings at the afforestation site sequestered about $2.5 \pm 0.001 \text{ Mg C ha}^{-1}$ at 15 MaP, at a stem carbon accumulation rate of $0.62 \text{ Mg C ha}^{-1} \text{ year}^{-1}$.

Discussion

In agreement with previous studies (e.g. Youkhana and Idol 2011; Kuyah et al. 2012a, b, 2013; Baumert and Khamzina 2015; Kuyah et al. 2016; Lin et al. 2017), the power function (Eq. 2) using basal diameter as the single predictor of TAGB, WAGB, LB and BGB provided the most accurate estimations for saplings of three out of the five afforestation species (*M. oleifera*, *J. curcas* and *A. occidentale*) tested in semi-arid Benin ($R^2 > 0.93$ and PRSE $< 30\%$). Large-scale (Ketterings et al. 2001) and global (Chave et al. 2014) tropical studies suggested incorporating locally derived H – D relationships into allometric equations to minimize prediction errors due to differing climate and soil conditions. However, the inclusion of the elaborated site-specific H – D relations did not improve the predictive capability of the corresponding model (Eq. 4) compared to that of the simple power model (Eq. 2), possibly due to the relatively narrow environmental gradients (e.g. rainfall, soil characteristics) at the afforestation sites (Noulèkoun et al. 2017a). Nevertheless, TAGB and WAGB of *J. curcas* and *A. occidentale* were estimated with similar precision by either approach, suggesting that the use of Eq. (4) obviates the need for destructive sampling and offers a good trade-off between accuracy, cost and practicability (Brown et al. 1989; Kuyah et al. 2012a). In line with previous findings on mature tree allometries (Youkhana and Idol 2011; Kuyah et al. 2012a, 2016), the addition of H (Eq. 3) in general did not improve model predictions for saplings in our study, with the exception of the AGB and BGB of the slowest growing species, *P. biglobosa*.

Statistical diagnostics of model performance using MAPE and MRE showed that high R^2 values alone do not necessarily guarantee precise estimates, as postulated earlier (Sileshi 2014; Baumert and Khamzina 2015) and as illustrated in our study by the higher errors associated with Eqs. (2) and (3) compared to Eq. (4) for *L. leucocephala*. Moreover, the model specification for various AGB fractions revealed less pronounced allometric relationships between LB and D than between TAGB or WAGB and D for several species (*M. oleifera*, *L. leucocephala* and *A. occidentale*). This is very likely due to the deciduousness caused by seasonal and environmental changes overshadowing the allometric impacts (Rubilar et al. 2010; Kuyah et al. 2013). The exclusion of LB, and hence considering WAGB only, increased model accuracy. This finding together with that of Baumert and Khamzina (2015) support the argument that deciduousness cannot be easily captured by allometric relations.

Given the dependence of the scaling exponent (β) between M and D on the relationship between H and D , the consideration of ontogenetic stages may improve the accuracy of biomass estimates (Pilli et al. 2006; Baumert and Khamzina 2015). At early ages and hence with an incomplete diameter series (Pilli et al. 2006), only the juvenile growth phase could be identified from our analysis of the H – D relation. The resulting negative allometric relationship ($c < 1$) observed between H and D for all the species implied that for the range of empirical diameters in the current study, the height growth rate was lower than the diameter growth rate. This follows the conclusion reported by Blujdea et al. (2012) for young plantations of winter-deciduous, broadleaved species in Romania. Notably, the

scaling exponent (c , 0.57) obtained for *J. curcas* in our study is very close to that (c , 0.55) determined for the same species across various management systems in Burkina Faso by Baumert and Khamzina (2015). The parameter c could therefore be considered as a proxy for predicting *J. curcas* biomass based on D for broader environmental gradients than recognised thus far. Despite the relatively small scale of the current study, the validation of the models using other datasets confirmed both the limited influence of environmental factors on the allometric parameters (α and β) and the applicability of the models to broader environmental conditions (Baumert and Khamzina 2015). Specifically, the WAGB and BGB estimates for *J. curcas* were validated using the independent dataset from Burkina Faso (Fig. 2). Collectively, these findings suggest that the H - D relationship and biomass estimates of *J. curcas* saplings are not significantly influenced by agro-ecological variability in West Africa, which is dominated by poor soil fertility and low-input cultivation. *J. curcas* has been generally reported as tolerant to drought and marginal soil conditions (Achten et al. 2010; Noulèkoun et al. 2017a).

The reverse exercise, i.e. feeding our data into previously reported allometric equations, revealed to what degree these equations might be applicable to the present case. For *J. curcas*, applying the equation Baumert and Khamzina (2015) developed for juvenile trees and those by Hellings et al. (2012) for trees with stems ranging from 4 to 16 cm in diameter to our empirical data produced reasonable estimates of WAGB and the MAPE and MRE values fell within the 95% confidence limits of the mean MAPE (20%) and MRE (3.4%; Fig. 3; Supplementary material, Appendix 3). Other equations available for *J. curcas* without consideration of ontogenetic stages showed poor fits, emphasizing that caution must be taken when applying published allometric functions to different datasets, without differentiating the age groups, even for the same species. Specifically, the function proposed by Achten et al. (2010) based on a greenhouse experiment with seedlings resulted in an underestimation of our WAGB data whereas equations by Baumert and Khamzina

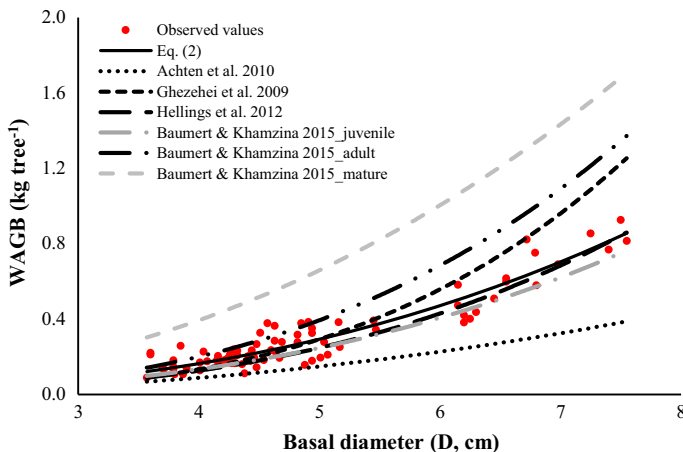


Fig. 3 Predicted woody aboveground biomass (WAGB) for *J. curcas* using the equations developed by Achten et al. (2010) for seedlings ($M = 0.0035D^{2.33}$), Ghezehei et al. (2009) ($M = 0.001D^{3.53}$), Hellings et al. (2012) ($M = 0.0019D^{3.03}$), Baumert and Khamzina (2015) for the juvenile growth stage ($M = 0.003D^{2.74}$), Baumert and Khamzina (2015) for the adult growth stage ($M = 0.003D^{3.03}$) and Baumert and Khamzina (2015) for the mature growth stage ($M = 0.016D^{2.31}$), compared to Eq. (2) ($M = 0.004D^{2.74}$). Further details on the equations, MAPE and MRE values are presented in Supplementary material, Appendix 3

(2015), previously developed for adult and mature trees, led to an overestimation (Fig. 3). When using the equation developed for the mature growth stage, the overestimation of sapling WAGB was particularly severe, as evidenced by an $MRE = 133\%$ (Fig. 3; Supplementary material, Appendix 3). In this regard, applying allometric equations to data beyond the initial calibration ranges is strongly not advised (Rothman 2002; Kuyah et al. 2012a; Sileshi 2014). Furthermore, the use of the generalized allometric equation developed by Brown (1997) for dry forests led to a substantial overestimation of TAGB ($404\% < MRE < 1235\%$) for all species, emphasizing that site-specificity needs to be accounted for in allometric models to increase their accuracy (Chave et al. 2014; Kuyah et al. 2016).

Our results suggest that the afforestation of degraded land with well-adapted and adequately managed tree species can significantly contribute to ecosystem carbon stocks in semi-arid regions. For instance, juvenile trees at the afforestation site accumulated stem carbon at a rate of $0.62 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, which is similar to the aboveground carbon accrual ($0.63 \text{ Mg C ha}^{-1} \text{ year}^{-1}$) in mature trees of African tropical forests (Lewis et al. 2009) and shows the potential of young forests in semi-arid environments. Moreover, the total (shoots and roots) productivity ($5.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$) was about three times greater than that of the 10-year-old fallow (shrubs and grasses) monitored in the vicinity of the afforestation site, and greater than that of the degraded cropland that is largely devoid of vegetation (Noulèkoun et al. 2017b). The stem carbon concentration in the afforestation species (41.5%) was also similar to that (41.5%) of the species studied by Weber et al. (2017) in the Sahelian and Sudanian ecozones of Niger. Moreover, the total biomass carbon stock of 2.8 Mg ha^{-1} measured in *J. curcas* plots 15 MaP in Benin exceeds that reported by Diédhiou et al. (2017) for a 2 year-old *J. curcas* plantation in Senegal (2.2 Mg C ha^{-1} with a stand density of 5000 trees ha^{-1}). Even greater accrual of carbon stocks was demonstrated by the other fast-growing species, *L. leucocephala* and *M. oleifera*. The AGB accounted for the largest proportion of the measured carbon stocks although in these juvenile trees, the foliage constituted up to 80% of AGB (*P. biglobosa*). As previously reported (e.g. Mokany et al. 2006; Kuyah et al. 2013; Noulèkoun et al. 2017b), BGB also represented an important carbon pool in the semi-arid region of Benin, accounting for 10–58% of the total biomass.

The overall RSR mean (0.35 ± 0.03) and median (0.31) values of the saplings in Benin were higher than the IPCC default value of 0.24 ± 0.02 for tropical hardwood species (Cairns et al. 1997) and the mean (0.32 ± 0.02) and median (0.28) values determined for juvenile, adult and mature trees in Kenyan agricultural landscapes (Kuyah et al. 2012b). Besides vegetation composition and site conditions, the observed differences might also be attributed to the lower water availability in semi-arid Benin, triggering increased root biomass allocation. The higher RSR could also be characteristic of the juvenile growth stage of the trees observed in Benin that favours a greater allocation of biomass to belowground while a lower RSR is expected to develop with age (Cairns et al. 1997; Mokany et al. 2006; Noulèkoun et al. 2017b). These current results suggest that in any case a RSR representative of the specific tree population and land-use system under study should be used when estimating root carbon stocks (Snowdon et al. 2000).

Conclusion

Allometric equations have been elaborated for predicting the AGB and BGB of saplings of five woody species of different genera planted on degraded land under variable water and nutrient supply in semi-arid Benin, West Africa. The conventional power equation provided the most conservative estimates of the biomass for most of the tested species. Adjusting the power equations for the height–diameter relations resulted in an accurate estimation of AGB based on the measured stem dimensions only, thus obviating the need for destructive sampling. For the slowest growing *P. biglobosa*, including the tree height improved the accuracy of the power model predictions.

The equations developed are applicable to saplings, and estimating the biomass of seedlings and mature plants would require a wider range of stem diameter data. Within the juvenile growth stage, the allometric relationships defined for *J. curcas* appeared valid for the estimation of its biomass over a wide range of agro-ecological conditions in semi-arid West Africa. In the absence of independent datasets for the other afforestation species, the sensitivity of their allometric equations to environmental gradients remains to be tested. Saplings accumulated a substantial amount of biomass and carbon at 15 MaP, by far exceeding the biomass in the traditional fallow system and demonstrating the potential of young forest plantations to offset CO₂ emissions. RSRs that are representative of the specific tree population and land-use system under study should be used when estimating root carbon stocks. These findings provide specific insight into the allometry of semi-arid afforestation species and can be used for site-adapted biomass predictions and fed into process-based models to estimate biomass and carbon stocks under a variety of environmental conditions.

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Sapling biomass allometry and carbon content in five afforestation species on marginal farmland in semi-arid Benin

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Appendix 1: Assessment of differences in the biomass-diameter relationship across harvest times and between treatments

We used the total biomass (i.e. aboveground biomass (AGB) + belowground biomass (BGB)) and the basal diameter of each tree to fit a nonlinear regression to the power-law function ($Y = \alpha X^\beta$) under the moderation of harvest times and treatments. The robust (vce) option in STATA 14 was used to estimate standard errors. The models used for a given species “i” are:

(1) For harvest times ($t_1 = 5$ MaP, $t_2 = 11$ MaP and $t_3 = 15$ MaP):

```
nl (TDM=cond(t1==1,{α1},cond(t2==2,{α2},{α3})) * D^(
cond(t1==1,{β1},cond(t2==2,{β2},{β3})))) if species== i, vce(cluster plotid)
```

(2) For treatments (tr1 = Control, tr2 = fertilization, tr3 = irrigation and tr4 = fertilization and irrigation):

```
nl (TDN= cond(tr1==1,{α1},cond(tr2==2,{α2},cond(tr3==3,{α3},{α4}))) * D^(
cond(tr1==1,{β1},cond(tr2==2,{β2},cond(tr3==3,{β3},{β4})))) if species==i, vce(cluster plotid)
```

where TDM is the total biomass, D is the basal diameter and vce (cluster plotid) is the option used for the robust estimation of the standard errors while accounting for pseudo-replication at plot level (plotid= plot identification).

A test of significant differences between intercepts and slopes was performed following each analysis. The results of these analyses are presented in Table 1 and 2.

Table 1 Allometric scaling coefficient (α) and exponent (β) for total biomass (kg tree^{-1}) and basal diameter (cm) relationships of five woody species at 5, 11 and 15 months after planting (MaP). The SEM is the standard error of the mean. The significance of the global test of intercepts and slopes is reported (Prob > F). A significance level of $p < 0.05$ was used as the threshold value

Species	5 MaP	11 MaP	15 MaP	Prob > F
<i>M. oleifera</i>				
α (SEM)	0.027 (0.011)	0.031 (0.018)	0.041 (0.018)	0.731
β (SEM)	2.085 (0.267)	1.706 (0.437)	1.795 (0.224)	0.632
<i>J. curcas</i>				
α (SEM)	0.022 (0.009)	0.151 (0.008)	0.003 (0.002)	0.241
β (SEM)	2.082 (0.274)	1.947 (0.351)	3.135 (0.336)	0.133
<i>L. leucocephala</i>				
α (SEM)	0.066 (0.025)	0.045 (0.014)	0.468 (0.189)	0.124
β (SEM)	1.806 (0.361)	2.030 (0.317)	0.999 (0.274)	0.052
<i>A occidentale</i>				
α (SEM)	0.045 (0.006)	0.026 (0.011)	0.031 (0.010)	0.205
β (SEM)	1.392 (0.218)	2.316 (0.387)	2.315 (0.188)	0.053
<i>P. biglobosa</i>				
α (SEM)	0.043 (0.005)	0.058 (0.012)	0.088 (0.033)	0.420
β (SEM)	1.334 (0.365)	01.217 (0.215)	1.407 (0.328)	0.690

Table 2 Allometric scaling coefficient (α) and exponent (β) for total biomass (kg tree^{-1}) and basal diameter (cm) relationships of five woody species under the control (C), fertilization (F), irrigation (I) and fertilization + irrigation (IF). The SEM is the standard error of the mean. The significance of the global test of intercepts and slopes is reported (Prob > F). A significance level of $p < 0.05$ was used as the threshold value

Species	C	F	I	IF	Prob > F
<i>M. oleifera</i>					
α (SEM)	0.027 (0.003)	0.029 (0.007)	0.008 (0.002)	0.012 (0.004)	0.006
β (SEM)	2.034 (0.065)	1.996 (0.142)	2.738 (0.147)	2.366 (0.196)	0.002
<i>J. curcas</i>					
α (SEM)	0.015 (0.006)	0.007 (0.001)	0.002 (0.001)	0.003 (0.000)	0.080
β (SEM)	2.230 (0.213)	2.792 (0.088)	3.321 (0.119)	3.195 (0.083)	0.024
<i>L. leucocephala</i>					
α (SEM)	0.090 (0.033)	0.071 (0.030)	0.046 (0.020)	0.021 (0.004)	0.161
β (SEM)	1.810 (0.311)	2.056 (0.299)	2.490 (0.312)	3.190 (0.158)	0.001
<i>A occidentale</i>					
α (SEM)	0.026 (0.003)	0.021 (0.003)	0.030 (0.007)	0.027 (0.004)	0.348
β (SEM)	2.240 (0.098)	2.539 (0.102)	2.354 (0.138)	2.459 (0.128)	0.054
<i>P. biglobosa</i>					
α (SEM)	0.044 (0.006)	0.052 (0.005)	0.089 (0.016)	0.028 (0.009)	0.148
β (SEM)	1.801 (0.226)	1.625 (0.274)	1.205 (0.274)	2.624 (0.257)	0.047

Note: There were no statistically significant differences between the intercepts (α) and slopes (β) of the three harvest times for all species. In contrast, results show that treatments influenced the biomass-diameter relationships of *M. oleifera*, *J. curcas* and *L. leucocephala* as evidenced by statistically significantly different slopes between treatments (Table 2). This implies treatment-specific equations could improve the predictive power of the allometric models. However, these equations would only be applicable to a very narrow range of growing conditions. Therefore, given the objective to develop allometric equations applicable to a large range of nutrient and water gradients, the data from all the harvest times and treatments were pooled.

Appendix 2: Carbon concentrations and biomass and carbon stocks in five afforestation species at 15 months after planting on degraded cropland in northern Benin. The SEM is the standard error of the mean. Stand density is 5,000 stems ha⁻¹

Species	Biomass fraction	Carbon (%)		Biomass (Mg ha ⁻¹)		Carbon stock* (Mg C ha ⁻¹)	
		Mean	SEM	Mean	SEM	Mean	SEM
<i>M. oleifera</i>	Foliage	41.4	0.5	0.89	0.07	0.37	0.000
	Branch	40.9	0.6	0.94	0.07	0.38	0.000
	Stem	41.8	0.9	3.36	0.20	1.41	0.002
	Coarse root	41.0	0.7	1.56	0.07	0.63	0.001
	Total	-	-	6.76	0.42	2.79	0.003
<i>J. curcas</i>	Foliage	42.1	0.8	1.91	0.12	0.80	0.001
	Branch	41.0	0.3	2.03	0.20	0.83	0.001
	Stem	40.3	0.5	1.40	0.06	0.56	0.000
	Coarse root	40.8	0.9	1.58	0.10	0.58	0.001
	Total	-	-	6.91	0.48	2.78	0.003
<i>L. leucocephala</i>	Foliage	42.7	0.7	2.98	0.25	1.27	0.002
	Branch	41.7	1.0	2.10	0.27	0.88	0.003
	Stem	42.8	0.6	2.75	0.17	1.18	0.001
	Coarse root	43.1	1.0	2.49	0.17	0.95	0.001
	Total	-	-	10.32	0.86	4.28	0.007
<i>A. occidentale</i>	Foliage	41.7	0.7	1.57	0.17	0.66	0.001
	Branch	41.3	0.3	0.74	0.12	0.31	0.000
	Stem	41.8	0.5	0.83	0.09	0.35	0.000
	Coarse root	42.3	0.6	0.50	0.06	0.19	0.000
	Total	-	-	3.65	0.43	1.50	0.002
<i>P. biglobosa</i>	Foliage	41.2	0.8	0.49	0.08	0.20	0.001
	Branch	40.9	-	0.02	0.01	0.01	-
	Stem	40.3	1.2	0.30	0.05	0.12	0.001
	Coarse root	43.8	0.7	0.54	0.08	0.22	0.001
	Total	-	-	1.36	0.23	0.56	0.002
Average for species	Foliage	42.0	0.4	1.65	0.11	0.69	0.000
	Branch	41.3	0.3	1.27	0.11	0.52	0.000
	Stem	41.5	0.3	1.87	0.13	0.77	0.000
	Coarse root	42.2	0.4	1.43	0.09	0.55	0.000
	Total	-	-	6.21	0.43	2.54	0.001

* Only coarse roots were considered for the estimation of root carbon stock

Appendix 3: Mean absolute percentage error (MAPE) and mean relative error (MRE) between observed and estimated values according to previously published allometric equations for *J. curcas*. M = woody aboveground biomass (kg tree⁻¹), D = diameter (cm)

Source	Diameter range (cm)	Equation	MAPE (%)	MRE (%)
Achten et al. (2010) for seedlings	-	$M = 0.0035 D^{2.33}$	47.3	-47.3
Ghezehei et al. (2009)	16-26	$M = 0.001 D^{3.53}$	26.7	4.2
Hellings et al. (2012)	4-16	$M = 0.0019 D^{3.03}$	22.0	-12.9
Baumert and Khamzina (2015) for juvenile plants	0-5.5	$M = 0.003 D^{2.74}$	21.6	-13.1
Baumert and Khamzina (2015) for adult trees	5.5-12.3	$M = 0.003 D^{3.03}$	42.9	38.6
Baumert and Khamzina (2015) for mature trees	12.3-21	$M = 0.016 D^{2.31}$	133.9	133.9

Note: For Ghezehei et al. (2009) equation, α was transformed to express biomass in kg tree⁻¹ and stem diameter in cm. Likewise, α was corrected to exclude the share of leaf biomass (43% of total aboveground biomass) for the Achten et al. (2010) equation (Hellings et al., 2012)

Article

Climate Change Sensitivity of Multi-Species Afforestation in Semi-Arid Benin

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Abstract: The early growth stage is critical in the response of trees to climate change and variability. It is not clear, however, what climate metrics are best to define the early-growth sensitivity in assessing adaptation strategies of young forests to climate change. Using a combination of field experiments and modelling, we assessed the climate sensitivity of two promising afforestation species, *Jatropha curcas* L. and *Moringa oleifera* Lam., by analyzing their predicted climate–growth relationships in the initial two years after planting on degraded cropland in the semi-arid zone of Benin. The process-based WaNuLCAS model (version 4.3, World Agroforestry Centre, Bogor, Indonesia) was used to simulate aboveground biomass growth for each year in the climate record (1981–2016), either as the first or as the second year of tree growth. Linear mixed models related the annual biomass growth to climate indicators, and climate sensitivity indices quantified climate–growth relationships. In the first year, the length of dry spells had the strongest effect on tree growth. In the following year, the annual water deficit and length of dry season became the strongest predictors. Simulated rooting depths greater than those observed in the experiments enhanced biomass growth under extreme dry conditions and reduced sapling sensitivity to drought. Projected increases in aridity implied significant growth reduction, but a multi-species approach to afforestation using species that are able to develop deep-penetrating roots should increase the resilience of young forests to climate change. The results illustrate that process-based modelling, combined with field experiments, can be effective in assessing the climate–growth relationships of tree species.

Keywords: climate sensitivity indices; *Jatropha curcas*; land degradation; *Moringa oleifera*; sapling growth; WaNuLCAS; West Africa

1. Introduction

There is an increasing recognition of the roles of forests and trees in mitigation and adaptation strategies to global climate change [1,2]. Tree planting can modify local climate through impacts on temperature, wind speed, and humidity; it can also influence the landscape–scale water balance, cloud cover and albedo, and contribute to global carbon sequestration [3–5]. In (sub-) tropical developing countries, re- and afforestation have been included in the portfolio of mitigation efforts

as a cost-efficient strategy to reverse the degradation of forests and to increase their atmospheric carbon uptake [1,2,6,7]. Although trees are central to many climate change adaptation and mitigation strategies, they are vulnerable (particularly in their early growth), to variation in solar radiation, rainfall, and temperature as determinants of potential evapotranspiration (ET_0). Changes in these climatic variables, particularly temperature increases and precipitation shortages leading to higher frequencies of extreme weather events (i.e., severe drought and intense rainfall), are expected to affect tree growth and challenge the sustainable management of forests and tree plantations [8–10].

Tree growth sensitivity to drought may be substantial in West African semi-arid zones, where water availability is one of the most limiting factors of plant growth, e.g., [11], and where extreme drought events are projected to become more frequent [12–14]. In this region, extreme drought events are associated with extended dry spells, low air humidity, high atmospheric evaporative demand, and high air temperatures [15], potentially increasing water stress in trees [13]. Droughts and dry spells are a major threat to the establishment and early growth of both tropical and temperate tree species [16–18], suggesting the need to assess the effects of climate variability on their growth. However, studies quantifying the relationships between these climatic factors and tree growth are lacking for tree plantations in the semi-arid tropics. This information is urgently needed to explore species' responses to past and current climate and evaluate the effects of climate change on tree growth [19].

If drought occurrences are exacerbated by global warming, it stands to reason that the sustainability of forests and plantations will largely depend on the physiological adaptations and changes in silvicultural management [18,20]. For example, Abdulai et al. [14] revealed drought vulnerability in a cocoa-based system in the forest–savanna transition zones of West Africa, despite the availability of subsoil water below a depth of 75 cm. This observation suggests that drought vulnerability may be related to trees' ability to develop sufficiently deep root systems [21]. Hartl-Meier et al. [22] found that among three tree species growing under similar temperate climate conditions, those with deep root systems benefited from the access to deep soil water, as reflected in their higher photosynthetic activity and continued biomass production during severe drought conditions. Therefore, the consideration of root systems in the analysis of climate–growth relationships may give new insights on species' responses to extreme climate events. Another plant strategy to avoid mortality under drought conditions is to shed leaves and reduce transpiration losses; such drought avoidance is likely to reduce the rate of photosynthesis and thus mean growth rates, but also reduce vulnerability [23].

Assessing the sensitivity and/or response of (early) tree growth to climate change requires the identification of the climate variables that most strongly influence tree growth or have the best predictive power in evaluating the early growth risks, e.g., Teets et al. [24]. However, experiments carried out in any given year to quantify climate–growth relationships of young trees may exhibit a sample of bad luck, lucky exceptions or be representative of 'normal' conditions at the test location, because experiments capture one (or a few) of the many possible weather (e.g., rainfall and temperature) sequences for this location. Early growth sensitivity of trees to predicted climate change cannot thus be directly derived from existing weather statistics because it is uncertain how tree transpiration, soil evaporation and temporal rainfall patterns interact, e.g., Raz-Yaseef et al. [25]. In this regard, we argue that well-calibrated tree–soil interaction models, simulating sapling growth responses for at least 30 years of weather data can help in (a) identifying the best predictors among a wide set of metrics that can be objectively derived from existing weather records; (b) evaluating where the years with experimental data are positioned within current climate variability according to the metrics with the highest predictive power identified in (a); and (c) using the results of (a) and (b) to assess the probability of success for given species at a given location under various location-specific climate change scenarios. Our study may be the first to test explicitly this generic approach to assess climate change risks for newly established dryland afforestation sites. The datasets stem from a site in a semi-arid zone of West Africa, where tree-based land restoration is high on the agenda and existing information is not sufficient to assess the robustness of afforestation option for a range of tree species [18,20,26].

Dendrochronology has been successfully used to analyze temporal and spatial climate–growth relationships for tree and shrub species in tropical and temperate forests [9,23,27,28]. However, dendrochronological applications may be inappropriate for young trees and compromised by problematic anatomical features such as missing, vague, discontinuous and false rings common in tropical species [29,30], thereby also restricting the use of biomass increments derived from tree-ring series [31,32]. An alternative approach to assessing the climate–growth relationships of saplings may be the use of process-based models in combination with field experiments. When supported by reliable soil–plant–climate databases and empirically derived relationships between environmental and plant eco-physiological parameters [33,34], process-based models can be used to investigate forest responses to climatic change and silvicultural management [35,36], as well as predict tree growth and productivity at both the plant and stand level. There have been few models capable of accurately simulating processes in tree-based agroecosystems.

The process-based Water, Nutrient and Light Capture in Agroforestry Systems (WaNuLCAS) model [35] has had various applications to improve the understanding of complex ecological processes in tree-based farming systems [35,37,38]. It has also been tested for its performance to simulate crop (e.g., *Pennisetum glaucum* L. and *Sorghum bicolor* L.) and tree (e.g., *Parkia biglobosa* Jacq. and *Vitellaria paradoxa* C.F. Gaertn) growth in agroforestry parklands in West Africa [39–41]. The aim of our research was to assess the climate sensitivity of two afforestation species—*Jatropha curcas* L. and *Moringa oleifera* Lam.—in the early stages of their development (i.e., the first two years of growth), decisive for the future growth [42] and also when plants are most sensitive to changes in water availability [43–45]. The two species have been subjects of silvicultural trials on degraded cropland in northern Benin [18,20,26]. The specific objectives were to (i) compare different indicators calculated from climate records to identify those with the greatest predictive power for the first two years of tree growth; (ii) quantify the climate–growth relationships of tree growth over the first two years, and (iii) test possible adaptation strategies to reduce the sensitivity of saplings to extreme climate events. Furthermore, we assessed the relevance of the empirical climate data vis-à-vis the long-term climatic variability in the study area based on the most influential climate indicators. We hypothesized that (i) there will be significant differences between the species' growth responses to climate indicators, particularly to drought-related indicators; (ii) drought sensitivity of sapling growth decreases over time, depending on the establishment of roots; and (iii) deepening of the rooting system may aid the adaptation of saplings to extreme drought conditions.

2. Materials and Methods

2.1. Study Area

Data for parametrization, validation, and simulations stemmed from a field experiment conducted during 2014–2015 at Pouri village (10°54'8.4" N, 1°4'47.4" E), Atacora region, northern Benin [18,20]. The region has been significantly affected by land degradation driven by deforestation and soil nutrient mining, which threatens the sustainability of forest and farming systems [18,46,47]. To combat land degradation, national and local projects to intensify forest cover, reclaim degraded lands and mitigate the effects of climate change (e.g., the project “10 Million Trees, 10 Million Souls”; <http://news.acotonou.com/h/61311.html>) through the planation of commercially important food (e.g., *M. oleifera*) and biofuel (e.g., *J. curcas*) tree crops have been carried out in the region [26,48].

The climate is semi-arid, characterized by two contrasting seasons, with one rainy season from April to October and a dry season for the rest of the year (Figure 1). The annual rainfall totaled 757 mm in 2014 and 833 mm in 2015, albeit both below the long-term (1981–2016) average of 1034 mm. The mean annual air temperature was 29 °C in 2014 and 28 °C in 2015. The area received an average solar radiation of 0.2 kW m⁻¹ ($\approx 914 \mu\text{mol m}^{-2} \text{s}^{-1}$ of photosynthetically active radiation) in 2014 and 2015. Historical patterns of change in precipitation, evapotranspiration, and air temperature showed a high inter-annual rainfall variability (676 < annual rainfall < 1509 mm; CV = 20%), along with extreme

dry (1985) and wet (1998) years, while inter-annual variations in evapotranspiration (CV = 4%) and temperature (2%) were smaller compared to that of annual precipitation (Appendix A, Figure A1).

The soil at the experiment site is an epileptic Plinthosol [49], compacted and limited at a depth of 50 cm by a lateritic hardpan. More details on the study site have been reported previously [18].

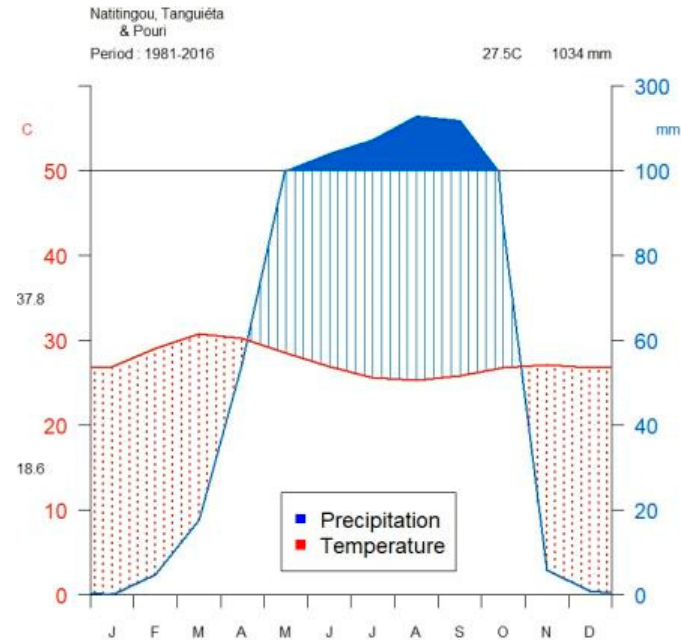


Figure 1. Climate diagram (according to Walter and Lieth [50]) based on 1981–2016 data of Natitingou (10°19' N and 1°23' E; altitude 460 m a.s.l), Tanguieta (10°37' N and 1°16' E; altitude 225 m a.s.l) and Pouri (10°54' N and 1°6' E; altitude 175 m.a.s.l) meteorological stations in the Atacora region, northern Benin. Top of the graph shows the long-term mean annual temperature and rainfall. The value at the top-left of the temperature axis is the mean of the average daily maximum temperature of the hottest month; the value at the bottom of the same axis is the mean of the average daily minimum temperature of the coldest month. Area shaded in blue indicates the moist period and area shaded in red shows the arid period. Area filled in blue indicates the period of excess water.

2.2. Experimental Design and Woody Species

The experiment compared the growth performance of saplings subjected to four management options, along an increasing gradient of resource availability: control (C; with neither irrigation nor fertilization), supplemental irrigation (I), fertilization (manure, F), and irrigation plus fertilization (IF). Irrigation was applied during the dry season only (November 2014–May 2015) at a rate of 0.5 L of water per sapling per day to satisfy 30% of the evaporative demand [18]. The saplings each received 72.5 mm of irrigation water and an additional 33 mm of rainfall during the dry season. Manure was applied in both rainy seasons, i.e., at 2.5 and 11 months after planting (MaP), at the amount of 1 kg per sapling (ca. 7.7 kg m⁻²). The manure consisted of composted cow and pig dung, and contained an average of 18.7% carbon (C), 1.2% nitrogen (N), and 0.8% phosphorus (P). No pesticide or fungicide was applied. Weed growth was controlled by frequent manual weeding.

Seeds of two multipurpose tree species, *Jatropha curcas* L. (physic nut, Euphorbiaceae) and *Moringa oleifera* Lam. (drumstick tree, Moringaceae), were germinated in a local nursery. Seedlings were planted in monospecific plots at the experimental site in July 2014 after 2.5–4 months, and were monitored over 15 months [18,20,26]. These local species were selected based on the fast growth rate of their shoots and roots in response to water and nutrient supply, as well as their socio-economic importance and increasing recent efforts to expand their plantation acreage in West Africa [18,26]. Each plot contained

48 seedlings with a 2 m × 1 m spacing, resulting in an initial stand density of 5000 trees ha⁻¹, which was used in the simulations.

2.3. Data Collection

Tree morphological properties and biomass were measured at the beginning and end of the 2014 and 2015 rainy seasons (i.e., 5, 11, and 15 MaP) on two to six saplings randomly selected per experimental plot [20,26]. After measuring the height (H, m) and stem diameter (D, cm), the selected trees were felled for total biomass determination, and that of the different tree fractions. The aboveground part was separated into leaves, branch, stem, and reproductive fractions. Roots were manually excavated, sectioned into coarse ($\phi > 2$ mm) and fine ($\phi < 2$ mm) fractions, and gently washed in a sieve to remove the soil. Subsamples of the harvested fractions were oven-dried at 75 °C until they reached a constant weight, and their dry mass was determined [20,26].

2.4. Modelling Analysis

2.4.1. Description of WaNuLCAS

The process-based WaNuLCAS model was developed by van Noordwijk and Lusiana [35] to improve the understanding of tree–soil–crop interactions in agroforestry systems, and runs on the STELLA (version 7.0) modelling environment software (isee systems Inc., Lebanon, PA, USA) linked to Microsoft Excel spreadsheets for data input and output, which allows modification by users [35]. WaNuLCAS simulates the daily tree growth as a function of resource (i.e., water, nutrient and light) availability at plot-scale. The plot is represented by a four-layer soil profile and four spatial zones, where trees (and/or crops) can be positioned (Figure 2).

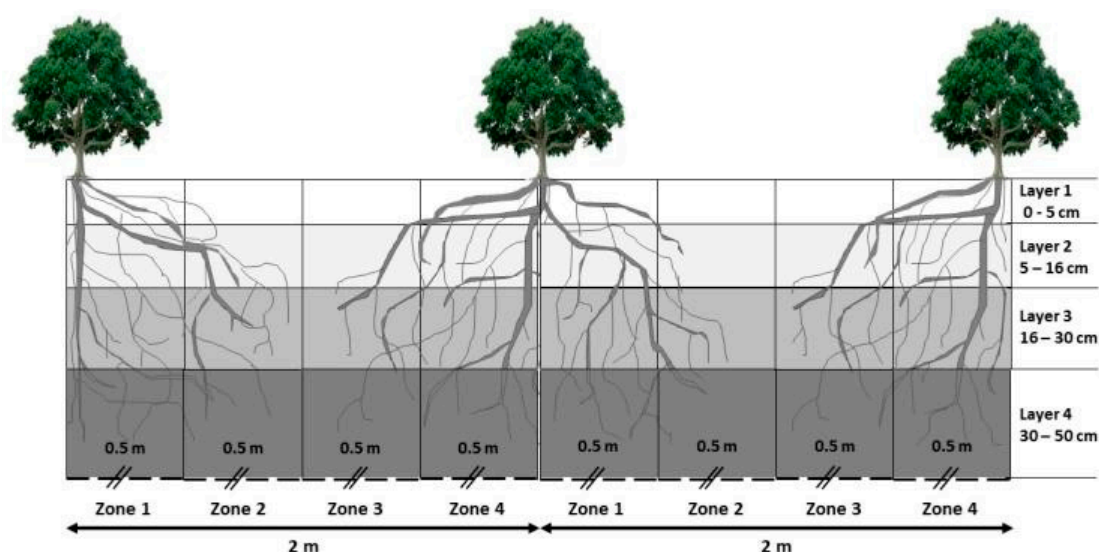


Figure 2. WaNuLCAS schematic presentation of the experimental plot layout, displaying its horizontal and vertical dimensions. Note: -//- indicate “broken” y-axis.

The model assumes homogenous site conditions within each of the four spatial zones. The emphasis of WaNuLCAS is on above- and belowground resource capture, based on leaf area and fine root length density interacting with resource supply as the basis for predicting interspecific complementarity and competition [51]. Belowground competition is described by calculating the demand and potential uptake of water and N and P nutrients using a zero-sink uptake model on the basis of the root length density. This assumes that the root uptake of water and nutrients is driven by plant demand, as long as the concentration of these resources at the root surface is above the limiting concentration, assumed to be zero under most conditions found in agricultural settings [52].

The demand for N uptake is defined by a “luxury uptake”, which assumes that growth will not be reduced until N content falls below 80% of the demand [51]. At the aboveground level, shading by trees is calculated as a function of the branch area index (BAI), leaf area index (LAI), and plant height in each zone. LAI-dependent light capture triggers photosynthesis, with carbon capture calculated on the dry weight basis. The distinction of the light captured by branch (BAI) and by leaves allows the model to account for tree shading when trees are leafless [51]. The model includes drought-induced litterfall and the re-emergence of leaves, controlled by phenological parameters.

The water balance of the system in WaNuLCAS includes rainfall, canopy interception, water evaporation from surface soil layers, water uptake by crops and trees, and leaching. Water is exchanged between the four zones by run-on and run-off. The vertical and horizontal transportation of water is also included [51]. Calculations of water infiltration into the soil profile follow a “tipping bucket” model [53]. Canopy interception is a function of ground cover (based on the LAI of trees and crops). Soil evaporation depends on both the ground cover and soil water content of the topsoil. Water uptake rate is driven by plant (i.e., trees and crops) transpirational demand, and is calculated based on soil and plant water potentials and the corresponding matrix flux potentials, determined following the methods of De Willigen et al. [52,54].

2.4.2. Input Data for WaNuLCAS

The WaNuLCAS model input data consist of weather data (daily rainfall, soil temperature, and potential evapotranspiration), soil parameters (texture; bulk density; saturated hydraulic conductivity; pH; and organic carbon, nitrogen, and phosphorus contents), tree management options (planting dates, amounts and timing of fertilization/organic material applications, intensity and timing of pruning), and tree library (i.e., growth parameters such as the length of the reproductive cycle, specific leaf area (SLA), growth rate; Supplementary materials, Tables S1 and S2).

Weather data: The 2014 and 2015 daily rainfall and air temperature data were made accessible by the Pouri weather station (Figure 1) located about 4 km away from the experiment site. Time-domain reflectometry (TDR) sensors (CS655, Soil Water Content Reflectometers, Campbell Scientific Ltd., Shepshed, Loughborough, LE12 9GX, UK) were installed at the experimental site at the beginning of the second rainy season to collect in-situ soil moisture and temperature data. Daily ET_0 data was generated using the FAO ET_0 calculator [55].

Soil parameters: Soil physical and chemical properties used to parameterize the WaNuLCAS model (Table 1) were set according to the four vertical layers of the model that correspond to the four layers obtained from the soil profile description (Figure 2). The Hodnett and Tomasella [56] pedotransfer function (PTF) in the WaNuLCAS model was used to generate soil hydraulic properties, representative of tropical soil conditions [57]. Default values of initial soil N (ammonium and nitrate) concentrations that were representative of a wide range of tropical cropping systems were used because no site-specific data was collected.

Table 1. Inputs of soil physical and chemical properties to parameterize the pedotransfer (PTF) module of WaNuLCAS.

Parameter	Soil Layer (cm)			
	0–5	5–16	16–30	30–50
Clay (%)	11.8	15.7	25.5	29.4
Silt (%)	31.4	35.3	33.3	37.3
Sand (%)	56.9	49.0	41.2	33.3
BD (g cm ⁻³)	1.5	1.5	1.6	1.6
pH-H ₂ O	5.3	5.2	5.7	5.8
TOC (%)	0.7	0.6	0.6	0.6
Ntot (%)	0.1	0.1	0.1	0.1
P (mg kg ⁻¹)	15.7	15.3	14.5	14.8
CEC (cmol kg ⁻¹)	4.7	6.0	5.2	5.3
Ksat (cm d ⁻¹)	73.2	18.4	207.7	232.4

Legend: BD: bulk density, TOC: total organic carbon, Ntot: total nitrogen, P: available phosphorus, CEC: cation exchange capacity, Ksat: saturated hydraulic conductivity. The data was obtained following a soil profile description conducted at the experimental site at the beginning of the trial in June 2014.

Crop and tree management: Field-collected data as described above was used for parameterization of this module. As the simulated system consists of trees only, the four horizontal zones of the model were set at equal widths of 0.5 m (Figure 2).

Tree growth parameters: Field-collected data was integrated into the “tree parametrization” Excel file (www.worldagroforestry.org/sea/Products/AFModels/wanulcas/downloadc.htm) to generate key growth parameters, including LAI, plant water potential, light extinction coefficient, and others, for use in WaNuLCAS [35,51]. The parameters permitted the simulation of aboveground growth and development, in particular the H, D, and aboveground biomass (AGB; kg m⁻²) production, subjected to the abovementioned climate, soil, and management factors. The biomass accumulation was simulated using the empirical allometric relationship between the biomass fractions (total AGB, leaf plus twig biomass, wood biomass, and litterfall) and stem diameter:

$$Y = aD^b \quad (1)$$

where Y is the biomass of a given fraction (kg tree⁻¹), D is the basal diameter (cm), and a and b are allometric coefficients.

The allometric coefficients (Table 2) were generated previously by Noulékoun et al. [26] using the experimental data. The root growth in all zones and layers was assumed to be constant, which is representative of a tree system with an equilibrium of root growth and root decay [51]. A maximum root length density was thus given as an input, following van Noordwijk et al. [51].

Table 2. Allometric intercepts (a) and slopes (b) of the biomass components [26] used to simulate the tree growth by WaNuLCAS.

Species	Biomass Fractions	a	b
<i>Jatropha curcas</i>	Total	0.004	2.93
	Stem	0.004	2.74
	Leaf + Twig	0.003	2.48
	Litterfall *	0.0002	3.29
<i>Moringa oleifera</i>	Total	0.010	2.36
	Stem	0.008	2.38
	Leaf + Twig	0.010	1.49
	Litterfall *	0.0002	3.29

* The model default values were used for litterfall allometric parameters.

2.4.3. Model Calibration, Validation, and Evaluation

The WaNuLCAS model was parametrized and calibrated with the two years of data gained from the fertilization (F) treatment. The data from the other treatments (C, I, and IF) were used for model validation. The three data collection periods (5, 11, and 15 MaP) served as comparison points between the measured and simulated values. During the calibration process, a sensitivity analysis was used to improve simulation results, following the method of Khasanah et al. [58]. Consequently, various parameters, such as the maximum LAI, maximum growth rate, and litterfall caused by drought, were modified for a more accurate reproduction of the observed values (Supplementary materials, Tables S1 and S2).

The model performance was evaluated by comparing the observed and simulated values of H, D, and AGB based on goodness of fit (GOF) (Appendix A, Table A1) statistical indicators proposed by Loague and Green [59], along with the coefficient of determination (R^2) of the linear relationship between the observed and simulated values (Figure 3). Based on these criteria, the accuracy of the model simulations was evaluated for its suitability to analyze the climate sensitivity of growth scenarios.

2.4.4. Climate–Growth Relationship Analysis

The model validated with data from the C treatment was used for the simulations, as this represents the common, low-input silvicultural practice in the study area. After calibrating the WaNuLCAS model to adequately capture the growth dynamics of saplings, 35 runs were performed, each covering two consecutive years over the historical climate period of 35 years (1981–2016), to quantify the strength of relationships between annual AGB growth and climate indicators [28]. These included indicators related to the rainfall amount (e.g., annual water deficit (AWD)), intensity (e.g., very wet days (R95p)), and temporal distribution (e.g., length of the longest dry spell (LDSP)) (Table 3).

Only climate indicators that showed low correlation ($r < 0.5$) were considered and assumed to influence the annual growth of plants. Air temperature was not directly included as an explanatory variable because the WaNuLCAS model does not include a representation of the direct effect of temperature on plant growth. Nevertheless, the effect of temperature was indirectly incorporated into the length of extreme dry periods (LEDP) and AWD through the ET_0 (Table 3).

The growth sensitivity of saplings to the prevailing climatic conditions was quantified by means of a linear mixed-effects model [28,60]. This approach was employed to account for the variance in growth between years. Climate indicators (Table 3) were used as fixed terms, i.e., as explanatory variables of the response variables (AGB) in the models, and the random term was the year. The model selection method [61] allowed the selection of the “best-fitting” model from a set of potential models fitted to each climate indicator separately, based on the difference in the corrected Akaike information criterion ($\Delta AICc$) between a null model (including intercept and random effect only) and the one-indicator models. The $\Delta AICc$ describes the effects of a given climate indicator on a model’s fit. A model was considered climate-sensitive when the ΔAIC was greater than two [28]. The preferred model was that with the lowest AICc and the highest $\Delta AICc$ [62]. The mixed models were fitted using the maximum likelihood estimation, restricted maximum likelihood estimation for slope estimates, and an autocorrelation structure (first-order autoregression (AR1)). The analysis was conducted in R version 3.4.3 [63] using the ‘nlme’ package [64].

Table 3. Climate indicators considered in the climate sensitivity analysis. The overall (1981–2016) value range of the climate indicators, and the value of the climate variable for the current climate (2014 and 2015) are presented along with their rank.

Parameters	Unit	Description	Definition	Range	2014	Rank **	2015	Rank **
AWD	mm	Annual water deficit	Difference between annual potential evapotranspiration (ET_0) and precipitation	155–1153	931	29/36	978	31/36
LDSP	Days	Length of the longest dry spell	Maximum number of consecutive days of no precipitation within the rainy season (April–October; Figure 1)	3–40	24	32/36	19	29/36
LEDP *	Days	Length of extremely dry period	Number of days within a year when daily maximum temperature >99th percentile (40° C) and no precipitation (Zhang et al. 2011)	0–42	8	30/36	42	36/36
LDS	Months	Length of dry season	Number of consecutive months within a year with less than 100 mm of rainfall (Wood et al. 2001)	5–10	10	36/36	9	35/36
LWS	Day	Length of the longest wet spell	Maximum number of consecutive rainy days within the rainy season (April–October; see Figure 1)	2–21	10	30/36	21	36/36
ATWP	mm	Annual total wet-day precipitation	Annual total precipitation from wet days (i.e., days with precipitation ≥ 1 mm) (Zhang et al. 2011)	670–1501	749	3/36	825	5/36
R95p *	mm	Very wet days	Annual total precipitation from days with precipitation >95th percentile (19 mm) (Zhang et al. 2011)	344–1096	395	4/36	424	7/36
R95pot	-	Total precipitation with respect to the R95p	Fraction of precipitation accounted for by the very wet days (R95p) (Zhang et al. 2011)	0.42–0.80	0.52	10/36	0.51	7/36

* The 95th and 99th percentiles of precipitation and temperature were identified from the historical (1981–2016) climate data. ** The ranking was done with regard to the 36 (i.e., 1981–2016) observations.

Table 4. Results of the model validation for two tree species based on the datasets from the control (C), irrigation (I), and irrigation + fertilization (IF) treatments based on the GOF criteria (Loague and Green [59]). Values in brackets represent the optimum value of the criteria. Values close to the optimum value of each criterion are indicated in bold.

Species	Growth Parameters	EF (1)	CD (1)	RMSE (0)	CRM (0)	ME (0)	R ² (1)
<i>Jatropha curcas</i>	Height (H, m)	0.72	0.71	6.02	0.00	0.16	0.80
	Diameter (D, cm)	0.72	2.48	11.12	-0.03	1.17	0.81
	Aboveground biomass (AGB, kg m ⁻²)	0.77	2.21	33.78	-0.04	0.19	0.83
<i>Moringa oleifera</i>	Height (H, m)	0.82	2.59	9.42	-0.03	0.40	0.97
	Diameter (D, cm)	0.70	1.76	12.94	-0.08	1.32	0.88
	Aboveground biomass (AGB, kg m ⁻²)	0.78	2.23	28.55	-0.09	0.13	0.88

EF: model efficiency; CD: coefficient of determination; RMSE: root mean square error; CRM: coefficient of residual mass; ME: maximum error; R²: coefficient of determination of linear regression between observed and simulated values.

Assuming that the annual growth and weather parameters across sequential years are not correlated [65], we compared climate effects in the first and second years of growth. Three indices of climate sensitivity were considered during the comparison [28]: (i) the highest $\Delta AICc$; (ii) the absolute value of the slope of the best model, which describes the strength and the direction of the relationship between the response and explanatory variables, as slopes were not bound to zero and can be either positive or negative; and (iii) the pseudo R^2 of the best model, which is a measure of the variance explained by a mixed model. The higher the value of any of these sensitivity indices, the higher the climate effects. Both the response and explanatory variables were standardized so that the slopes had a common unit and were comparable. The R^2 GLMM function of the 'MuMIn' library in R 3.4.3 was used to compute the R^2 value of each one-indicator mixed model [66].

2.4.5. Scenario Description

Scenario analyses were performed to evaluate the impact of rooting depth on the biomass production of saplings under two contrasting water stress conditions, considering the spatial variation in soil depth and depending on the landscape position and the depth of the lateritic hardpan, and possible root penetration of the hardpan to capture leached rainfall [18] (personal field observation). Two soil and rooting depth scenarios were thus built by keeping the total root length constant and by changing the initial rooting depth (50 cm; Figure 2) by +50%. This resulted in (i) a shallower rooting depth (33.3 cm) with obliquely oriented roots and (ii) a deeper rooting depth (75 cm) with vertically penetrating roots. Water stress was imposed during the simulations by using the climate data of the two consecutive years with the highest (i.e., severe water stress or extreme dry condition) and lowest (i.e., mild water stress or extreme wet condition) cumulative water deficits.

3. Results

3.1. Simulation of Tree Height, Diameter, and Aboveground Biomass

The outputs of the model calibration revealed strong linear relationships ($R^2 > 0.8$) between the simulated and observed values of H, D, and AGB (Figure 3) for both species. The tree growth increments were also reasonably well reproduced by the model (Appendix A, Figure A2). The overall evaluation of the model indicated a good fit between the model estimates and empirical values for the key parameters, as evidenced by the satisfactory values of model efficiency (EF), coefficient of determination (CD), coefficient of residual mass (CRM), and maximum error (ME) (Figure 3).

The reproducibility was reduced due to the diameter shrinking (RMSE ca. 7–12%) and the biomass loss as litterfall (root mean square error [RMSE] ca. 23–26%) during the dry season, which resulted in the overestimation of D and AGB by the model at this point in time (Figure 3; Appendix A, Figure A2).

The model validation (with the independent datasets from the C, I, and IF treatments) showed similar results to that of the model calibration, albeit with a reduced GOF compared to that of the calibration (Table 4). Furthermore, the comparison of the relative increment in growth parameters induced by the treatments between the model predictions and the field observations revealed that the predicted values aligned well with the field measurements for both species (Supplementary Materials, Table S3). Hence, the results of the calibration and validation revealed the model's suitability for the envisaged scenario analyses.

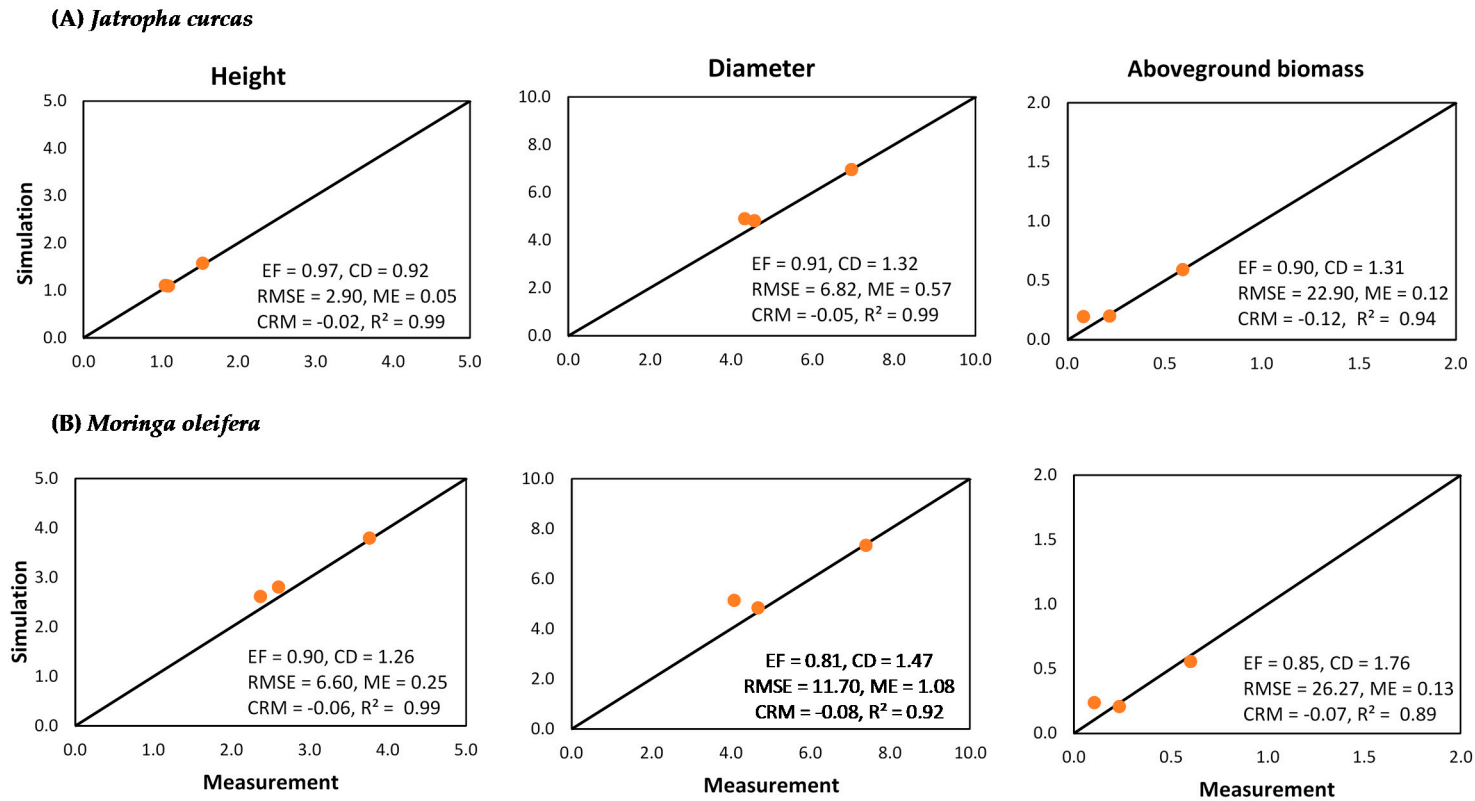


Figure 3. Relationships between simulated and observed values of height (m), stem diameter (cm) and aboveground biomass (kg m^{-2}) for *J. curcas* and *M. oleifera* during calibration. The data from the fertilization treatment (F) were used. The lines are the 1:1 lines. EF: model efficiency; CD: coefficient of determination; RMSE: root mean square error; CRM: coefficient of residual mass; ME: maximum error; R^2 : coefficient of determination of linear regression between observed and simulated values.

3.2. Climate–Growth Relationships of the Afforestation Species

The annual AGB growth varied substantially over the simulation period as a result of the inter-annual rainfall and evapotranspiration variability inherent to the reference data (Figure 4 and Appendix A, Figure A1), confirming the common climate–growth relationship.

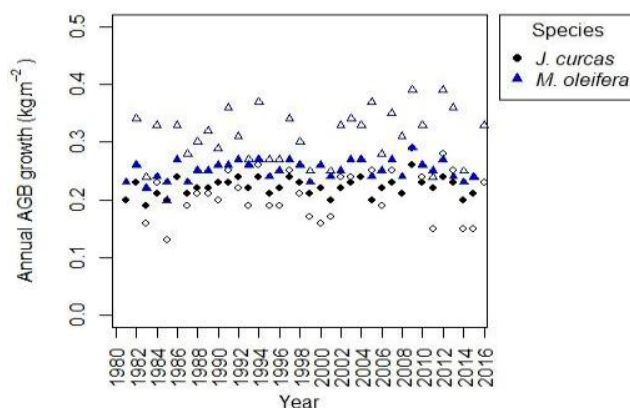


Figure 4. Variation in the predicted annual aboveground biomass (AGB, kg m^{-2}) growth for *J. curcas* and *M. oleifera*. Apart from the years 1981 and 2016, every year was used twice in the simulation, either as year 1 (filled symbols) or year 2 (open symbols) year.

The observed variance reflected differences in the climate effects of a given year, when used either as year one or year two during the two-year simulation period. Differences in climate–growth patterns between the species are evident in Figure 4. For instance, the annual AGB growth of *M. oleifera* was higher in year two than in year one in 86% (30/35) of the runs, indicating that the annual growth is likely to be more influenced by climatic conditions in year two. In contrast, the biomass growth of *J. curcas* was dependent on the climatic conditions in both years (one and two; Figure 4).

The computed climate indicators can be further categorized into two groups: (i) drought-related indicators (AWD, LDSP, LEDP and LDS) and (ii) wetness-related indicators (LWS, ATWP, R95p and R95pot). The values of the drought-related indicators for the two years in which tree growth data were collected (2014 and 2015) were in the upper range of the 1981–2016 data (representing its maximum as shown by the year 2014 ranking for LDS), whereas the wetness-related indicators were in the lower quartile (Table 3). Furthermore, the results of the linear modeling analyses revealed that the AGB growth of both species was influenced by the AWD, LDS, LDSP, and ATWP (Table 5).

Table 5. Mixed effect models comparisons for *J. curcas* and *M. oleifera*, showing the most important climate indicators along with the corresponding climate sensitivity indices.

Variables	<i>Jatropha curcas</i>			<i>Moringa oleifera</i>		
	ΔAICc	Slope	R^2	ΔAICc	Slope	R^2
LDSP ₁	12.22	−0.63	0.39	9.33	−0.58	0.33
LDSP ₂	9.91	−0.59	0.35	8.31	−0.57	0.31
LDS ₁	2.27	−0.43	0.18	2.16	−0.42	0.18
LDS ₂	12.16	−0.63	0.39	9.13	−0.58	0.33
AWD ₁	6.02	−0.53	0.27	5.05	−0.5	0.24
AWD ₂	14.92	−0.67	0.44	11.98	−0.63	0.38
ATWP ₁	3.60	0.46	0.21	2.96	0.45	0.20
ATWP ₂	10.44	0.60	0.36	8.32	0.57	0.31

Note: ΔAICc is the corrected Akaike Information Criterion; R^2 is the pseudo coefficient of determination. Description of the climate variables is provided in Table 2. Subscripts accompanying the climate variables stand for year one (1) and year two (2).

Across the years, drought-related indicators (AWD, LDS, and LDSP) best explained the variations in the annual AGB growth, as reflected in their overall high $\Delta AICc$ and R^2 values. The most important and extensive climate factor influencing the annual biomass growth for both species was the AWD, as evidenced by the highest values of the sensitivity indices (Table 5). The AWD was the easiest to calculate, as it only required ET_0 and annual rainfall, rather than details of the temporal rainfall distribution. The biomass growth was inversely (slopes < 0) linked to the drought-related indicators, but the ATWP had a positive effect on the AGB growth of both species. The AWD had the strongest negative effect (highest slope values) on the sapling growth (Table 5).

The strength of climate–growth relationships and the identity of climate indicators in the best-fit models varied between years one and two (Table 5). The climate sensitivity was greatest in the second year of tree growth for all of the important climate indicators, except for the LDSP, which had the strongest effects on annual growth during the first year. Overall, *M. oleifera* tended to be less sensitive to climate than *J. curcas*, but the observed differences in sensitivity were too subtle to draw general statements considering the threshold ($\Delta AICc > 2$) used to indicate a significant climate effect.

3.3. Simulated Effect of Rooting Depth on Sapling Biomass under Contrasting Water Stress Conditions

The simulation results revealed that the rooting depth influenced the biomass production of saplings (Figure 5), and the magnitude of this effect varied between the water stress scenarios. After the first two years of growth and irrespective of the species, AGB was 13–72% higher for deep-rooted plants compared to the shallow-rooted ones. The relative change in AGB induced by the deep rooting depth was greater under extreme dry conditions (i.e., 1984–1985) compared to that under extreme wet conditions (i.e., 2004–2005) (Figure 5). For instance, the relative change for *J. curcas* was 72% and 27% for the 1984–1985 and 2004–2005 runs, respectively. The enhanced biomass growth of saplings with deeper roots was related to an increased water uptake and canopy interception, reduced runoff and drainage, and thus increased the soil available water and its use by saplings (Figure 6).

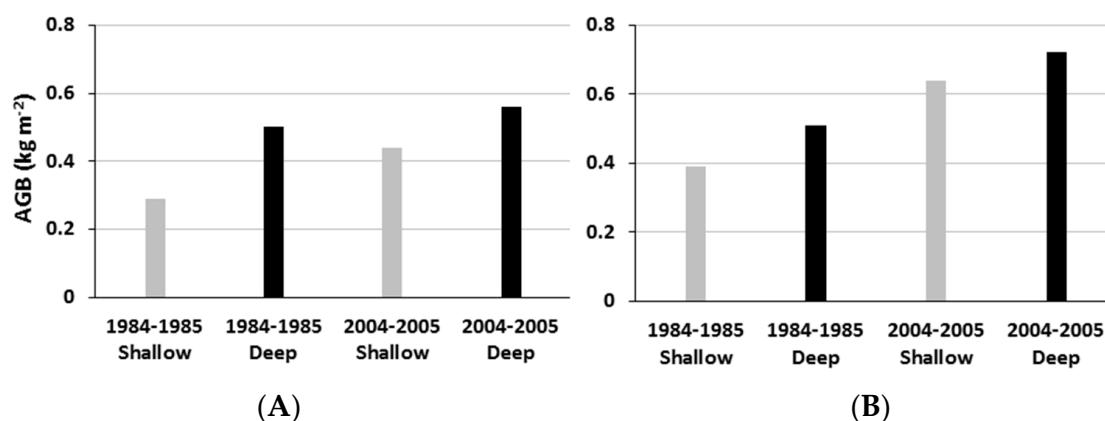


Figure 5. Simulated effects of rooting depth (Shallow vs. Deep) on aboveground biomass (AGB, kg m⁻²) under severe (1984–1985) and mild (2004–2005) water stress for (A) *Jatropha curcas* and (B) *Moringa oleifera*.

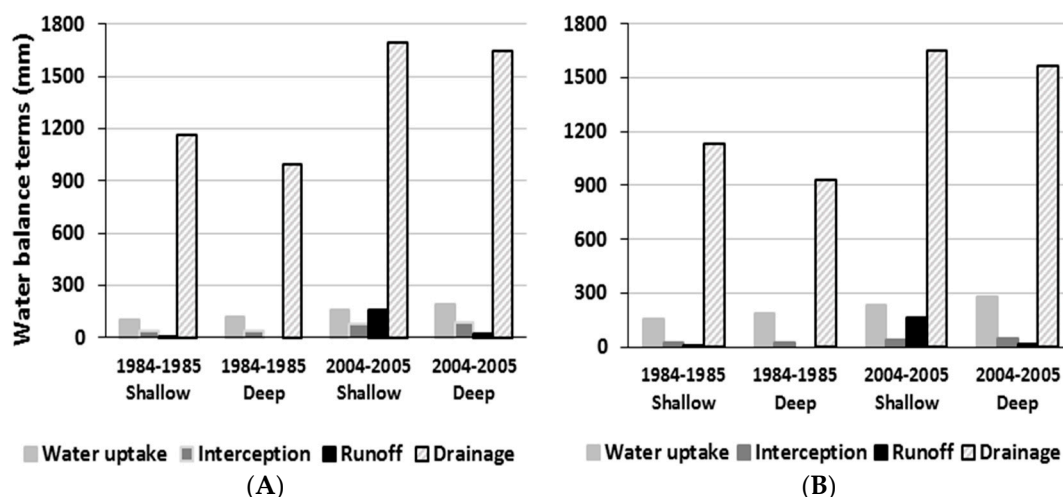


Figure 6. Water balance terms (mm) for two rooting depths (Shallow and Deep) under severe (1984–1985) and mild (2004–2005) water stress for (A) *Jatropha curcas* and (B) *Moringa oleifera*. Cumulative values over the two-year simulation period are presented.

4. Discussion

Climate change is likely to affect trees in the early growth stage, altering the long-term productivity of forests and plantations [42,44,67]. Although climate–growth relationships have been quantified for mature trees of several tropical and temperate species [9,29,68], much remains unknown regarding the sensitivity of tree growth during the early stages of development in semi-arid areas. In this study, we used a generic approach of climate sensitivity assessment that combines field experiments and modelling as an alternative to the traditional dendrochronology technique. First, we calibrated and validated the process-based model WaNuLCAS based on the empirical tree growth data. Second, we quantified the effects of climate variability on the predicted annual biomass increment, based on the most influential climate indicators. We also assessed the relevance of the empirical climate data to historical simulations based on the frequency distribution of the long-term climate indicator data (Table 3). Our results revealed drought-related indicators as the best predictors, which enabled to quantify their effects on sapling growth. Our approach has an advantage over the dendrochronological analysis because it uses actual biomass increment rather than biomass increment derived from tree-rings as recently suggested [31,32], thereby avoiding challenges associated with problematic anatomical features of tree rings common in tropical trees [29,30].

4.1. Model Performance

In accordance with previous studies [41,57,69,70], the range of the GOF statistics and the high correlation between the simulated and observed growth parameters for both the calibration (Figure 3) and the validation (Table 4) are indicative of the ability of the WaNuLCAS model to reproduce the early growth dynamics of the tested afforestation species with an acceptable accuracy and precision. A R^2 value of 0.5, CD value of 0.5–2, and EF value above 0.5 represent a good predicted–to–observed relationship [69]. However, the high values of the RMSE for AGB during the model calibration and the reduced GOF during the model validation indicated that not all growth limitations occurring under field conditions were adequately captured through simulations [39]. Most of the discrepancies between the simulations and empirical evidence arose from the limited capacity of the model to reproduce the monitored drought-induced trunk shrinkage and litterfall during the dry season. Shrinking tree diameters are not represented in the current version of the model, although they are known at both the diurnal and seasonal time scales [71]. Drought-induced litterfall is included in the model by a water potential threshold and a waiting period before new leaves emerge [72], but an accurate

parametrization requires data beyond what is available for the site. While dry-season leaf shed is characteristic for drought-deciduous tree species, its accounting in our simulations resulted in large reductions of the total height rather than D and AGB (results not shown), implying that tree canopy and height are more influenced by this process than D and AGB in the WaNuLCAS model. The lack of calibrated litterfall data may have caused the poor fit of the predicted D and AGB, albeit only during the dry season [57]. Despite these deviations between the observed and simulated values during the dry season, the well-reproduced growth patterns and accurate prediction of D, H, and AGB at the end of the growing seasons (Appendix A, Figure A2) are a sufficient basis for further analyses of plant growth.

4.2. Climate Sensitivity of Afforestation Species

The predicted AGB growth series showed strong variations over the years (Figure 3), indicative of the influence of climate on the early growth of tree plantations [68]. Although both species have a semi-deciduous phenology and are fast growing and drought tolerant [18], their predicted annual growth responses to climate variability differed (Figure 3), confirming our hypothesis that the responses are species specific. This is likely due to the differences in stress tolerances [73] and/or allometry. Species differences in climate–growth responses have been reported for older trees of winter-deciduous broad-leaved species (*Fagus sylvatica* L. and *Quercus petraea* Matt.) under a temperate climate [68]. Together, these findings suggest that caution must be taken when parametrizing growth models according to plant functional types [5].

Water availability emerged as the primary driver of the climate sensitivity of trees in the early stages of growth in semi-arid areas. Similar climate–growth relationships were previously found for temperate tree species [68,74] and for shrub species across the tundra biome [28]. Annual biomass accumulation declined with annual water deficit, the length of the dry season, and the length of the longest dry spell, but increased with the annual total wet-day precipitation (Table 5). This supports our hypothesis that drought-related indicators negatively affect biomass growth in particular. The negative climate–growth relationships with drought-related indicators suggested that drought-reduced sapling growth occurred not only due to reductions in the total amount of precipitation and subsequent longer dry seasons (e.g., AWD), but also due to variability in the distribution of rainfall (e.g., the LDSP). This outcome is reminiscent of the findings by Elliott et al. [9], which showed that the distribution of precipitation is more influential on the radial growth of deciduous tree species than the amount.

Increased aridity (AWD) had the strongest negative influence on the growth of saplings, suggesting that the projected increase in aridity in northern Benin [75] may result in a substantial decrease in growth. For instance, the predicted AGB of *J. curcas* after two years of growth was 0.34 and 0.49 kg m⁻² under extreme (highest AWD) and mild (lowest AWD) drought conditions, respectively, which represents a potential 31% loss in AGB growth. Applying the same calculations for *M. oleifera* resulted in a 14% loss in growth if the aridity is increased. These estimates are obviously to some extent simplified, as AWD is not the only climate factor that is likely to change in the future; however, they do highlight the relative importance of water limitation for the early growth of tree plantations and hence for the planted afforestation efforts in the region.

The influence of drought on tree growth and the identity of climate drivers were not uniform between years. In year one, the duration of the LDSP in the rainy season had the best predictive power, while in year two, the annual water balance (here, the difference between precipitation and ET₀) was the best predictor for both species (Table 5). This supports our hypothesis that the climate sensitivity to ‘immediate’ drought is stronger at the very early stages of tree growth, when root systems are not yet fully established [43–45], compared to later stages where the water balance dominates results. Sensitivity to AWD and LDS was greater in the second year compared to the first. This could be attributed to the increased tree water use and consequent reduction in soil available water related to increased canopy interception and water drainage as a function of tree growth in the WaNuLCAS model [51]. For instance, the water use efficiency of *J. curcas*, defined as the water uptake to total

rainfall ratio, was 4% in year one and 10% in year two under the most extreme historical drought scenario (1984–1985). This implies that the same AWD or LDS would result in more water stress in year two than in year one. Hence, the climatic factors related to the amount of precipitation showed greater sensitivity in year two, whereas greater sensitivity to LDSP, which describes the distribution of precipitation, was more evident in year one.

Just as empirical data gives insights in the credibility of model predictions, the current analysis of sensitivity of tree growth to a range of rainfall metrics can help to better judge the representativeness of the empirical data regarding climate variability in the study area. The year 2014 had the longest LDS of the available climate data set for the test site, while the AWD and LDSP of both years were in the upper quartiles (Table 3). The values of the wetness-related indicator (ATWP) were in the lowest quartile for both years. Apparently, the years in which experimental data were collected were already foreboding what climate change predictions point out as a ‘new normal’ for the study area: less predictable rain, with more extremes on both the high and the low end [12,13]. Therefore, the tree performance measured during the two years is probably a conservative estimate of what can be expected in years closer to the current average values and is more representative of the expected growth under projected climate conditions.

4.3. Effects of Rooting Depth on Biomass Growth under Extreme Dry Conditions

The simulation results showed that deeper rooting depth was an advantage to sapling growth of both species under extreme dry conditions (Figure 5). Moreover, the AGB at the end of year two was greater for deep-rooted than shallow-rooted saplings in both extreme dry and wet conditions. The improved performance can be attributed to enhanced tree water use under deep rooting depth conditions as a result of increased water uptake and canopy interception, and reduced water drainage and runoff (Figure 6). The relative increase in AGB, induced by the deep rooting depth, was greater under severe water stress compared to mild water stress, suggesting that deep-rooted saplings are less sensitive to extreme drought than shallow-rooted saplings. Similarly, Coulibaly et al. [41] has reported that tree species with deep rooting systems are less vulnerable to water deficits. These results can be attributed to the fact that during extreme drought conditions, deep rooted saplings take advantage of their access to deeper soil horizons, which could result in increased photosynthetic activity and continued biomass production, as reported by Hartl-Meier et al. [22] for beech (*Fagus sylvatica* L.) and larch (*Larix decidua* Mill.) under a temperate climate.

4.4. Replicability of the Approach

Where trees of a wide range of ages can be found in a local environment of interest, dendrochronological analysis can, in combination with climate records, be used for assessing the effects of climate change on young forests. In the absence of such, the combination we used of experiments, model calibration and identification of the local climate metric with the best predictive skill can improve the value of experiments and increase their interpretation, at the interface of climate change mitigation and adaptation strategies.

5. Conclusions

The WaNuLCAS model was successfully calibrated and validated to simulate sapling growth of two afforestation species in semi-arid northern Benin. Although the stem diameter and biomass predictions during the dry season were poorly simulated due to the limited ability of the model to reproduce trunk shrinkage and litterfall during this period, the overall outputs of the model calibration and validation were satisfactory. The model application to simulate the early growth of the afforestation species under past climate conditions permitted the quantification of the climate sensitivity of sapling growth.

The aboveground biomass growth was most sensitive to water availability, as evidenced by the negative relationships between growth and drought-related indicators, and the positive growth

response to annual total wet-day precipitation. The distribution, rather than the total amount, of precipitation was the main factor limiting sapling growth at the very early stages of growth (year one), when tree root systems are not yet well established. Given the projected increase in variability of precipitation distribution, extended arid conditions, and longer dry spells in West Africa, the current results suggest that increased aridity could play an increasingly important role in limiting future tree establishment and forest growth. Based on the observed species-specific responses to climate variability and the importance of root depth in buffering the negative effects of extreme drought on sapling growth, a multi-species afforestation system with species that are able to develop deep-penetrating root systems may increase the resilience of plantations to climate change.

The current results illustrate that process-based modelling combined with field experiments can be effective in integration of multi-source data to assess the climate–growth relationships of tree species. Further verification of the simulation results under field conditions, through dendrochronological and rhizological studies, would be needed to develop confidence in the application of WaNuLCAS for climate–growth analyses.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2071-1050/10/6/1931/s1>, Table S1: Tree parameters used for simulating the growth of *Jatropha curcas* L. in WaNuLCAS; Table S2: Tree parameters used for simulating the growth of *Moringa oleifera* Lam. in WaNuLCAS; Table S3: Relative increment in height (m), diameter (cm), and aboveground biomass (ABG, kg m⁻²) in response to fertilization, irrigation and fertilization plus irrigation as observed and as simulated by WaNuLCAS.

Author Contributions: F.N., J.P.A.L., J.B.N., and A.K. conceived and designed the experiments. F.N. and J.B.N. conducted the experiments and field data collection. F.N., N.K., and M.v.N. performed modeling and statistical analyses. All the authors contributed to the writing of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix

Table A1. Statistical criteria proposed by Loague and Green [59] to evaluate model performance.

Criteria	Symbol	Formula	Acceptable Range	Optimum Value
Model efficiency	EF	$\frac{(\sum_{i=1}^n (O_i - O_{mean})^2 - \sum_{i=1}^n (P_i - O_i)^2)}{\sum_{i=1}^n (O_i - O_{mean})^2}$	≤1	1
Coefficient of determination	CD	$\frac{\sum_{i=1}^n (O_i - O_{mean})}{\sum_{i=1}^n (P_i - O_{mean})}$	0.5–2 *	1
Maximum error	ME	$Max P_i - O_i _{i=1}^n$	≥0	0
Root mean square error	RMSE	$\left(\sum_{i=1}^n \frac{(P_i - O_i)^2}{n} \right)^{1/2} \times \frac{100}{O_{mean}}$	≥0	0
Coefficient of residual mass	CRM	$\frac{(\sum_{i=1}^n O_i - \sum_{i=1}^n P_i)}{\sum_{i=1}^n O_i}$	≤1	0

P_i , predicted value; O_i , observed value; O_{mean} , mean of the observed value. * The range for CD proposed by Walker et al. [57].

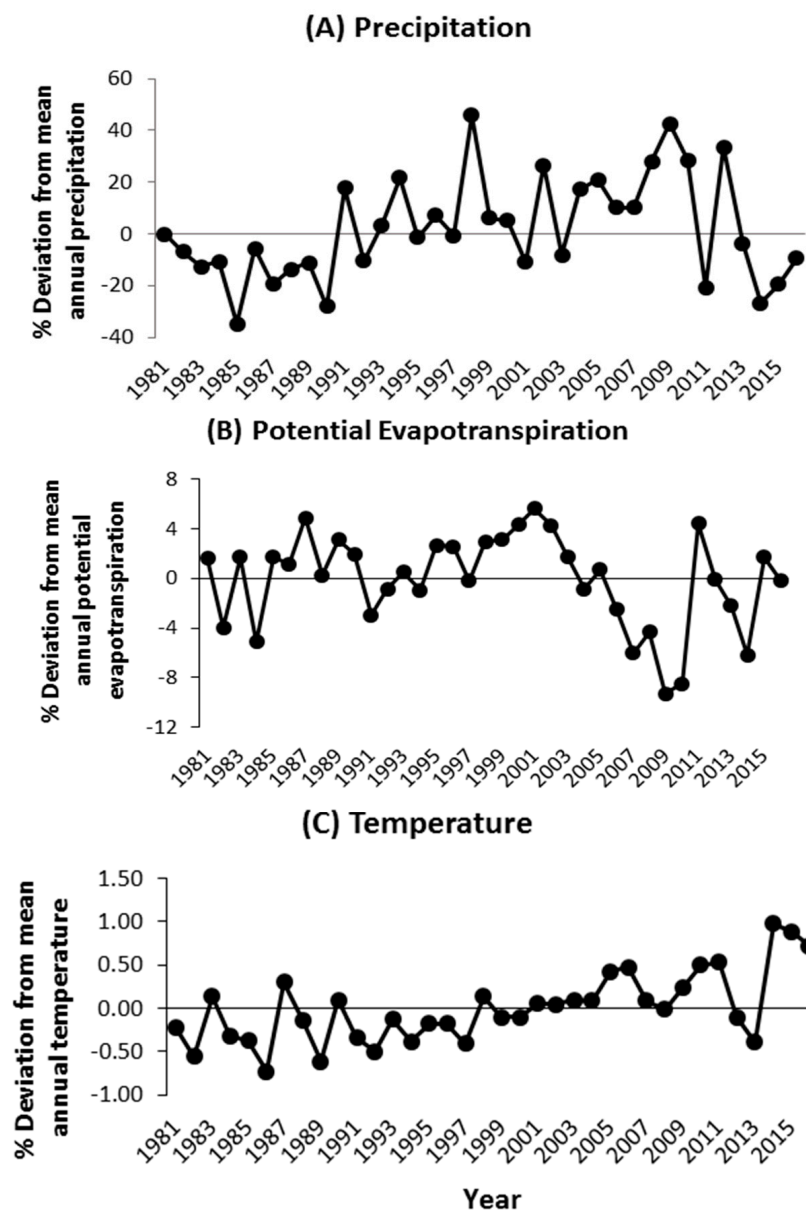


Figure A1. Relative changes in the annual rainfall (mm), annual potential evapotranspiration (mm), and air temperature ($^{\circ}\text{C}$) between 1981 and 2016 compared to the long-term historical means presented in Figure 1.

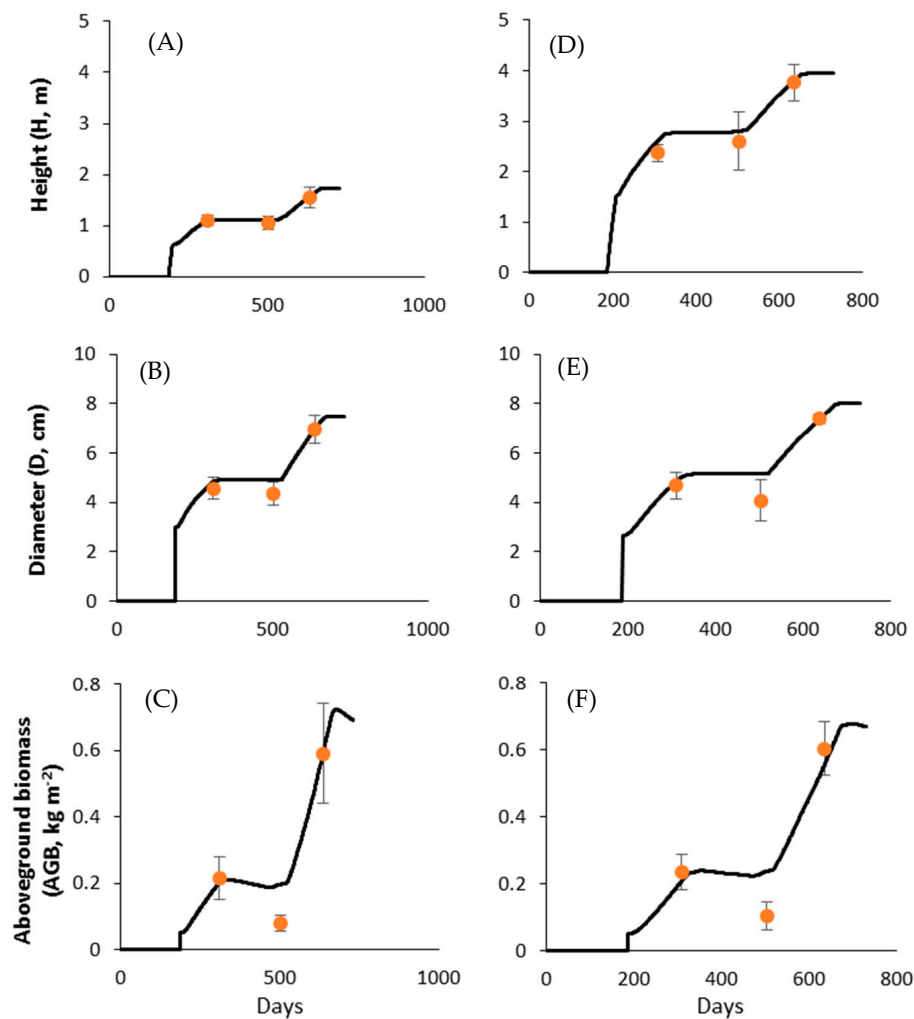


Figure A2. Simulated height (H, m), stem diameter (D, cm), and aboveground biomass (AGB, kg m⁻²) dynamics for *Jatropha curcas* (A–C) and *Moringa oleifera* (D–F) during calibration for which the empirical datasets from the fertilization treatment was used. The three comparison points (circles) represent the three harvest times (i.e., 5, 11, and 15 months after planting). Vertical bars are standard errors of the mean. Seedling planting time was defined at 186 Julian days in the Water, Nutrient and Light Capture in Agroforestry Systems (WaNuLCAS) model.

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Table S1 Tree parameters used for simulating the growth of *Jatropha curcas* L. in WaNuLCAS. C = calibrated values; L = values from literature; M = measured values; D = default values from the “WaNuLCAS tree parametrization” Excel file, except for default values of root parameters, which were derived from the “WaNuLCAS” Excel file

Parameter	Description	Unit	<i>Jatropha curcas</i>		
			Default value	Value used in simulation	Determination
Growth Stage	Length of vegetative cycle	days	365	365	D
	Length of generative cycle	days	90	90	D
	Earliest day to flower in a year	Julian day	305	305	D
	Latest day to flower in a year	Julian day	195	195	D
	Initial stage	-	0.10	0.10	D
	Stage after pruning	-	0.15	1.00	L
Growth	Max. growth rate	kg m ⁻²	0.02	0.007	C
	Fraction of growth reserve	-	0.025	0.025	D
	Leaf weight ratio	-	0.70	0.50	M
	Specific leaf area	m ² kg ⁻¹	7.00	25.40	M
	Water requirement for dry matter production	l kg ⁻¹	300	300	D
	Tree growth follows rubber tree rules?	-	0.00	0.00	D
Fruit	Fruit growth follows oil palm rules?	-	0.00	0.00	D
	Fraction biomass allocated to fruit	-	0.25	0.08	L
Canopy	Max. canopy height above bare stem	m	1.50	1.76	M
	Ratio between canopy width and height	-	0.50	0.48	C
	Max. canopy radius	m	1.50	1.62	M
	Maximum leaf area index	-	5.33	3.00	C
	Ratio leaf area index min. and max.	-	0.50	0.36	L

Table S1 continued

Parameter	Description	Unit	<i>Jatropha curcas</i>		
			Default value	Value used in simulation	Determination
Light capture	Relative light intensity at which shading starts to affect tree growth	-	0.50	0.50	D
	Extinction light coefficient	-	0.70	0.50	C
Rain interception	Rainfall water stored at leaf surface	mm	1.00	1.00	D
Tree Water	Coefficient related to tree root conductivity	cm day ⁻¹	0.00002	0.00002	D
	Plant potential for max. transpiration	cm	-1500	-1500	D
	Plant potential for min. transpiration	cm	-4500	-4500	D
N₂ Fixation	Type of N ₂ fixation	-	0.00	0.00	D
	Proportion of N from atmosphere	-	0.00	0.00	D
	Fraction of reserve pool for N ₂ fixation	-	0.00	0.00	D
	Dry weight cost for N ₂ fixation	-	0.005	0.005	D
	Responsiveness of N ₂ fixation to N stress	-	0.00	0.00	D
N Concentration	N concentration in carbohydrate reserves	g g ⁻¹	0.11	0.11	D
	N concentration in leaf component	g g ⁻¹	0.025	0.0099	M
	N concentration in twig component	g g ⁻¹	0.008	0.0158	M
	N concentration in wood component	g g ⁻¹	0.005	0.0175	M
	N concentration in fruit component	g g ⁻¹	0.015	0.015	D
	N concentration in root component	g g ⁻¹	0.01	0.0142	M
P Concentration	P concentration in carbohydrate reserves	g g ⁻¹	0.0055	0.01	C
	P concentration in leaf component	g g ⁻¹	0.001	0.0004	L
	P concentration in twig component	g g ⁻¹	0.00	0.0038	L

Table S1 continued

Parameter	Description	Unit	<i>Jatropha curcas</i>		
			Default value	Value used in simulation	Determination
	P concentration in wood component	g g ⁻¹	0.00	0.0019	L
	P concentration in fruit component	g g ⁻¹	0.001	0.0047	L
	P concentration in root component	g g ⁻¹	0.001	0.0014	L
Litterfall	Litterfall caused by drought	day ⁻¹	0.10	0.008	C
	Threshold value for litterfall due to drought	-	0.70	0.70	D
	Reducing factor for N of litterfall	-	0.85	0.85	D
	Reducing factor for P of litterfall	-	0.85	0.85	D
Litter quality	Lignin fraction of litterfall	-	0.20	0.1584	L
	Lignin fraction of pruned biomass	-	0.20	0.1683	L
	Lignin fraction of root	-	0.20	0.1395	L
	Polyphenol fraction of litterfall	-	0.05	0.0371	L
	Polyphenol fraction of pruned biomass	-	0.05	0.0314	L
	Polyphenol fraction of root	-	0.05	0.0968	L
Allometric Branching (Aboveground)	Apply allometric equation?	-	1.00	1.00	-
	Intercept for total biomass equation	kg	0.012	0.004	M
	Power for total biomass equation	cm ⁻¹	2.336	2.930	M
	Intercept for branch biomass equation	kg	0.008	0.004	M
	Power for branch biomass equation	cm ⁻¹	2.315	2.740	M
	Intercept for Leaf and twig biomass equation	kg	0.004	0.003	M
	Power for leaf and twig biomass equation	cm ⁻¹	2.373	2.480	M
	Intercept for litterfall equation	kg	0.03	0.000	D

Table S1 continued

Parameter	Description	Unit	<i>Jatropha curcas</i>		
			Default value	Value used in simulation	Determination
	Power for litterfall equation	cm ⁻¹	3.094	3.290	D
	Wood density	kg m ⁻³	336.3	336.3	L
Roots	Root tip diameter	cm	0.10	0.10	D
	Max. root length density in layer1-zone1	cm cm ⁻³	2.00	0.035637	L
	Max. root length density in layer1-zone2	cm cm ⁻³	1.20	0.907471	L
	Max. root length density in layer1-zone3	cm cm ⁻³	0.72	0.787833	L
	Max. root length density in layer1-zone4	cm cm ⁻³	0.00	0.001	L
	Max. root length density in layer2-zone1	cm cm ⁻³	1.50	0.001	L
	Max. root length density in layer2-zone2	cm cm ⁻³	0.90	0.196004	L
	Max. root length density in layer2-zone3	cm cm ⁻³	0.54	0.496373	L
	Max. root length density in layer2-zone4	cm cm ⁻³	0.00	0.001	L
	Max. root length density in layer3-zone1	cm cm ⁻³	0.60	0.001	L
	Max. root length density in layer3-zone2	cm cm ⁻³	0.36	0.085274	L
	Max. root length density in layer3-zone3	cm cm ⁻³	0.216	0.081456	L
	Max. root length density in layer3-zone4	cm cm ⁻³	0.00	0.001	L
	Max. root length density in layer4-zone1	cm cm ⁻³	0.20	0.001	L
	Max. root length density in layer4-zone2	cm cm ⁻³	0.12	0.001	L
	Max. root length density in layer4-zone3	cm cm ⁻³	0.072	0.038183	L
	Max. root length density in layer4-zone4	cm cm ⁻³	0.00	0.001	L

Note: Literature values from Tjeuw (2017)

Table S2 Tree parameters used for simulating the growth of *Moringa oleifera* Lam. in WaNuLCAS. C = calibrated values; L = values from literature; M = measured values; D = default values from the “WaNuLCAS tree parametrization” Excel file, except for default values of root parameters, which were derived from the “WaNuLCAS” Excel file

Parameter	Description	Unit	<i>Moringa oleifera</i>		
			Default value	Value used in simulation	Determination
Growth Stage	Length of vegetative cycle	days	183	183	D
	Length of generative cycle	days	90	90	D
	Earliest day to flower in a year	Julian day	210	210	D
	Latest day to flower in a year	Julian day	360	360	D
	Initial stage	-	0.10	0.10	D
	Stage after pruning	-	0.10	0.10	D
Growth	Max. growth rate	kg m ⁻²	0.036	0.008	C
	Fraction of growth reserve	-	0.025	0.025	D
	Leaf weight ratio	-	0.70	0.50	M
	Specific leaf area	m ² kg ⁻¹	10.5	16	C
	Water requirement for dry matter production	l kg ⁻¹	300	300	D
	Tree growth follows rubber tree rules?	-	0.00	0.00	D
Fruit	Fruit growth follows oil palm rules?	-	0.00	0.00	D
	Fraction biomass allocated to fruit	-	0.080	0.08	D
Canopy	Max. canopy height above bare stem	m	3.30	3.30	D
	Ratio between canopy width and height	-	0.50	0.23	C
	Max. canopy radius	m	2.00	2.00	D
	Maximum leaf area index	-	3.00	3.00	C
	Ratio leaf area index min. and max.	-	0.50	0.33	C

Table S2 continued

Parameter	Description	Unit	<i>Moringa oleifera</i>		
			Default value	Value used in simulation	Determination
Light capture	Relative light intensity at which shading starts to affect tree growth	-	0.80	0.80	D
	Extinction light coefficient	-	0.86	0.86	D
Rain interception	Rainfall water stored at leaf surface	mm	1.00	1.00	D
Tree water	Coefficient related to tree root conductivity	cm day ⁻¹	0.00002	0.00002	D
	Plant potential for max. transpiration	cm	-1500	-1500	D
	Plant potential for min. transpiration	cm	-4500	-4500	D
N₂ Fixation	Type of N ₂ fixation	-	0.00	0.00	D
	Proportion of N from atmosphere	-	0.00	0.00	D
	Fraction of reserve pool for N ₂ fixation	-	0.00	0.00	D
	Dry weight cost for N ₂ fixation	-	0.00	0.00	D
	Responsiveness of N ₂ fixation to N stress	-	0.00	0.00	D
N Concentration	N concentration in carbohydrate reserves	g g ⁻¹	0.22	0.22	D
	N concentration in leaf component	g g ⁻¹	0.025	0.013	M
	N concentration in twig component	g g ⁻¹	0.015	0.020	M
	N concentration in wood component	g g ⁻¹	0.01	0.015	M
	N concentration in fruit component	g g ⁻¹	0.023	0.023	D
	N concentration in root component	g g ⁻¹	0.01	0.011	M
P Concentration	P concentration in carbohydrate reserves	g g ⁻¹	0.022	0.022	D
	P concentration in leaf component	g g ⁻¹	0.003	0.003	D
	P concentration in twig component	g g ⁻¹	0.002	0.002	D

Table S2 continued

Parameter	Description	Unit	<i>Moringa oleifera</i>		
			Default value	Value used in simulation	Determination
	P concentration in wood component	g g ⁻¹	0.001	0.001	D
	P concentration in fruit component	g g ⁻¹	0.002	0.002	D
	P concentration in root component	g g ⁻¹	0.001	0.001	D
Litterfall	Litterfall caused by drought	day ⁻¹	0.100	0.008	C
	Treeshold value for litterfall due to drought	-	0.90	0.70	C
	Reducing factor for N of litterfall	-	0.85	0.85	D
	Reducing factor for P of litterfall	-	0.85	0.85	D
Litter quality	Lignin fraction of litterfall	-	0.20	0.20	D
	Lignin fraction of pruned biomass	-	0.20	0.20	D
	Lignin fraction of root	-	0.20	0.20	D
	Polyphenol fraction of litterfall	-	0.05	0.05	D
	Polyphenol fraction of pruned biomass	-	0.05	0.05	D
	Polyphenol fraction of root	-	0.05	0.05	D
Allometric Branching (Aboveground)	Apply allometric equation?	-	1.00	1.00	-
	Intercept for total biomass equation	kg	0.010	0.010	M
	Power for total biomass equation	cm ⁻¹	2.360	2.360	M
	Intercept for branch biomass equation	kg	0.008	0.008	M
	Power for branch biomass equation	cm ⁻¹	2.380	2.380	M
	Intercept for leaf & twig biomass equation	kg	0.010	0.010	M
	Power for leaf & twig biomass equation	cm ⁻¹	1.490	1.490	M
	Intercept for litterfall equation	kg	0.000	0.000	D

Table S2 continued

Parameter	Description	Unit	<i>Moringa oleifera</i>		
			Default value	Value used in simulation	Determination
	Power for litterfall equation	cm ⁻¹	3.290	3.290	D
	Wood density	kg m ⁻³	262	262	D
Roots	Root tip diameter	cm	0.10	2.00	D
	Max. root length density in layer1-zone1	cm cm ⁻³	2.00	2.00	D
	Max. root length density in layer1-zone2	cm cm ⁻³	1.20	1.20	D
	Max. root length density in layer1-zone3	cm cm ⁻³	0.72	0.72	D
	Max. root length density in layer1-zone4	cm cm ⁻³	0.00	0.00	D
	Max. root length density in layer2-zone1	cm cm ⁻³	1.50	1.50	D
	Max. root length density in layer2-zone2	cm cm ⁻³	0.90	0.90	D
	Max. root length density in layer2-zone3	cm cm ⁻³	0.54	0.54	D
	Max. root length density in layer2-zone4	cm cm ⁻³	0.00	0.00	D
	Max. root length density in layer3-zone1	cm cm ⁻³	0.60	0.60	D
	Max. root length density in layer3-zone2	cm cm ⁻³	0.36	0.36	D
	Max. root length density in layer3-zone3	cm cm ⁻³	0.216	0.216	D
	Max. root length density in layer3-zone4	cm cm ⁻³	0.00	0.00	D
	Max. root length density in layer4-zone1	cm cm ⁻³	0.20	0.20	D
	Max. root length density in layer4-zone2	cm cm ⁻³	0.12	0.12	D
	Max. root length density in layer4-zone3	cm cm ⁻³	0.072	0.072	D
	Max. root length density in layer4-zone4	cm cm ⁻³	0.00	0.00	D

Table S3 Relative increment in height (m), diameter (cm), and aboveground biomass (kg m⁻²) in response to fertilization, irrigation and fertilization plus irrigation as observed and as simulated by WaNuLCAS. Average values of the three harvest times are presented

Treatment effect	Height (m)		Diameter (cm)		Aboveground biomass (kg m ⁻²)	
	Measured	Simulated	Measured	Simulated	Measured	Simulated
<i>Jatropha curcas</i>						
Fertilization (F)	0.10	0.10	0.48	0.54	0.13	0.12
Irrigation(I)	0.08	0.02	0.30	0.05	0.09	0.01
Irrigation plus fertilization (IF)	0.13	0.15	0.53	0.81	0.18	0.17
<i>Moringa oleifera</i>						
Fertilization (F)	0.03	0.15	0.51	0.37	0.07	0.03
Irrigation(I)	0.00	0.06	0.15	0.12	0.01	0.02
Irrigation plus fertilization (IF)	0.08	0.11	0.61	0.29	0.07	0.17

Reference

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