FUNCTIONAL TRAITS, DROUGHT PERFORMANCE, AND THE DISTRIBUTION OF TREE SPECIES IN TROPICAL FORESTS OF GHANA

Lucy Amissah

Thesis committee

Promotor
Prof. Dr G. M. J. Mohren
Professor of Forest Ecology and Forest Management
Wageningen University

Co-promotors
Prof. Dr L. Poorter
Personal chair in the Forest Ecology and Forest Management Group
Wageningen University

Dr B. Kyereh
Senior Lecturer, College of Agriculture and Natural Resources
Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

Other members
Prof. Dr N.P.R. Anten, Wageningen University
Dr M.D. Swaine, University of Aberdeen, Scotland
Prof. Dr R.G.A. Boot, Tropenbos International, Wageningen, The Netherlands
Dr E.M. Veenendaal, Wageningen University

This research was conducted under the auspices of the C.T. de Wit Graduate School for Production Ecology and Resource conservation (PE&RC)

Functional traits, drought performance, and the distribution of tree species in tropical forests of Ghana

Lucy Amissah

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr M.J. Kropff,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Monday 15 September 2014
at 1:30 p.m. in the Aula.

Lucy Amissah
Functional traits, drought performance, and the distribution of tree species in tropical forests of Ghana
200 pages.
PhD thesis, Wageningen University, Wageningen, NL (2014)
With references, summaries in Dutch and English
ISBN 978-94-6257-072-6

To Kodwo, Marilyn, Emmanuela and Michelle

Abstract

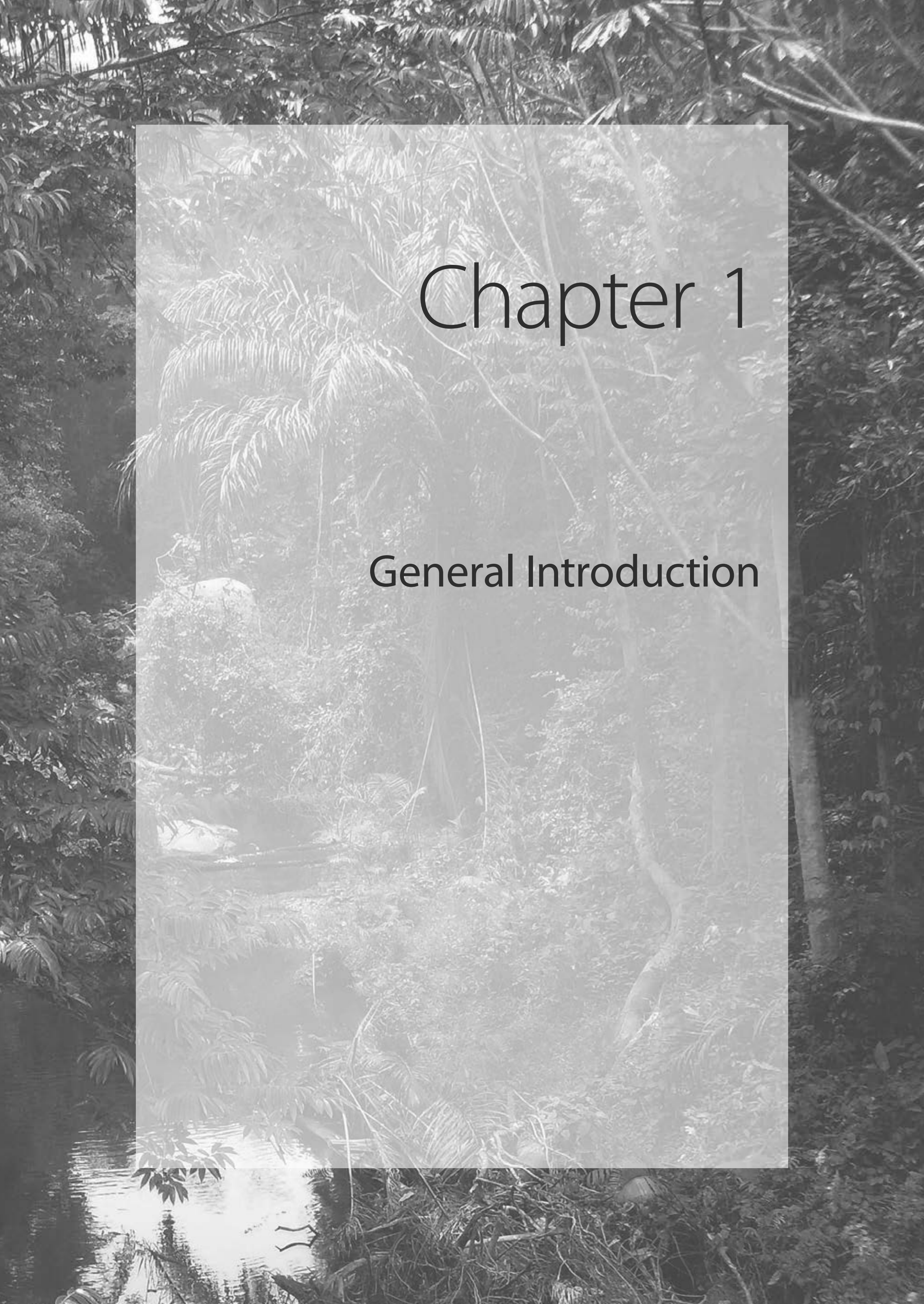
Tropical forests occur along a rainfall gradient where annual amount, the length and intensity of dry season vary and water availability shapes therefore strongly the distribution of tree species. Annual rainfall in West Africa has declined at a rate of 4% per decade, and climate change models predict a further reduction in rainfall and an increase in frequency and intensity of drought. This will have large consequences for the diversity, composition and distribution of tropical tree species. Understanding the factors that shape tree species distribution will help to understand current forest functioning and to predict the potential impact of climate change on forests.

In this thesis, I used a combination of forest inventory data, greenhouse and field experiments to determine the responses of 10-23 species to drought and shade, and analyse the underlying mechanisms. I addressed 4 questions: (1) What is the relative importance of rainfall and temperature on tree species distribution? (2) How do tree species acclimatise to drought and shade in terms of their physiology, morphology, growth and survival? (3) What morphological and physiological traits determine species drought performance and distribution? (4) How do seedling survival, growth and physiology vary between dry and wet forests, and does drought tolerance and growth determine species distribution along the rainfall gradient?

Forest inventory data showed that the distribution of 95% of 20 species was significantly associated with annual rainfall, 60% with rainfall seasonality, 45% with isothermality and 40% with temperature seasonality. Thus, a reduction in annual rainfall, and an increase in frequency and intensity of drought as predicted by climate change models may affect the distribution of many tree species. A greenhouse experiment indicated that shade facilitated the survival of seedlings subjected to drought, rather than reducing it. This contrasts with the trade-off hypothesis that suggests a stronger impact of drought in shade conditions. Across 23 species, I found a trade-off between drought avoidance (by a deciduous leaf habit during drought) and physiological drought tolerance (by having tough and persistent tissues that allow plants to function during drought) strategies. These strategies were closely associated with species' shade tolerance and growth rates. A suite of functional traits predicted drought survival and tree species position on the rainfall gradient. Across species, drought survival was enhanced by having less biomass allocation to transpiring leaves, a low leaf area

per unit plant mass, and by dense and tough leaf and wood tissues that allow plants to function during drought. The field experiment showed that drought survival (and growth) in the dry forest relative to the wet forest correlated negatively with species position on the rainfall gradient. Hence, species that survive and grow relatively well in dry forests are found at the drier end of the rainfall gradient. This suggests that species sensitivity to low water availability determines the distribution of tree species. The predicted increase in drought frequency and intensity may, therefore, cause a shift in the distribution of tree species in tropical forests.

Contents



Chapter 1

General Introduction

Tropical forests and their relation with rainfall, water availability and temperature

Tropical forests are found in climates that vary in total annual rainfall, length and severity of dry seasons, and mean annual temperature (Lieberman 1982, Orians 2000). On a global scale primary productivity, tree species distribution and diversity of plant communities have been found to correlate with rainfall gradient and moisture availability (Boyer 1982, Curie & Paquin 1987, Engelbrecht & Kusar 2003). At the regional and local scales in wet and moist tropical forests a number of studies have found that tree species occurrence, distributions and diversity strongly correlate with **annual rainfall** (Hall & Swaine 1981, Gentry 1988, Condit 1998, Swaine 1996, Bongers *et al.* 1999). This suggests that plant water availability may be one of the main factors influencing habitat associations of tropical trees, shrubs and herbs (Bongers *et al.* 1999, Swaine 1996, Veenendaal & Swaine 1998, Webb and Peart 2000). The rainfall gradient is a complex gradient, where rain, soil fertility, light and pest pressure change in concert. In addition, other environmental factors such as temperature may influence the distribution of tree species along the rainfall gradient (Toledo *et al.* 2012). For instance high temperature implies higher evapotranspiration, which can affect the water balance of plants. Both from a theoretical and applied point of view there is the need to understand what environmental variables determine the distribution patterns of tree species. This becomes even more urgent in the face of climate change as findings can help to predict the vulnerability of forest communities to climate change.

Soil fertility is one of the factors that co-vary with the rainfall gradient (Swaine 1996). Wet forest soils are generally low in pH and in base saturation and cation exchange due to more leaching in wet forest soils compared to dry forest soils (Veenendaal & Swaine 1998, Murphy & Lugo 1986). In a study in Bolivia that focused on the distribution (occurrence) of 100 tree species in relation to climatic and edaphic factors, 47% of species studied responded to soil fertility, whereas another 44% responded to soil texture (Toledo *et al.* 2012). However, in controlled experiment in Ghana and Panama only few species showed a growth response to soil fertility and no evidence of home soil advantage was found for most of the species studied (Veneendaal *et al.* 1996c, Brenes-Arguedas *et al.* 2008). Additionally, field experiments in Ghana and in Panama have provided only weak evidence that soil fertility may affects the distribution of species over other factors (Swaine *et al.* 1997). Other studies have found correlation between seedling growth and nutrient; in La Selva, Costa Rica seedling growth correlated with soil nutrients in 48% of 522 woody species studied in an understory of a wet forest (Holste *et al.* 2011).

Pest and pathogens are biotic filters that vary along the rainfall gradient and affects species distribution. It has generally been hypothesized that herbivore and pathogen pressure is greater in wet tropical forest than in dry tropical forests because of perhumid and more benign conditions (Connell 1971, Coley & Barone 1996). As a result, wet forest species are expected to have evolved better defense mechanisms against pests than dry forest species. Empirical evidence of the existence of gradient in pest pressure along the rainfall gradient has been found in some studies (e.g. Brenes-Arguedas *et al.* 2009) but not in others (e.g. Baltzer & Davies 2012). None of these two studies found evidence for distribution-based differences in vulnerability to herbivores (Brenes-Arguedas *et al.* 2009, Baltzer & Davies 2012) and therefore both have concluded that pest is not as strong a determining factor in shaping species distribution as is rainfall seasonality (Brenes-Arguedas *et al.* 2009).

Light availability co-varies with the rainfall gradient and may contribute to factors that shape species distribution (Veenendaal *et al.* 1996c, Agyeman *et al.* 1999, Brenes-Arguedas *et al.* 2011). Light availability, especially in the understorey decreases towards wetter forest as a result of variation in the phenology of the canopy trees (Brenes-Arguedas *et al.* 2011). Ecophysiological tolerances to shade combined with the effects produced by competition by pest, pathogens and herbivores can also contribute to species distribution along rainfall gradients (Engelbrecht & Kusar 2003, Baltzer *et al.* 2008, Kusar *et al.* 2009).

Seasonality of rainfall has a strong influence on temporal patterns of primary and secondary production, decomposition and tree species distribution in tropical forests (Orians 2000, Engelbrecht & Kusar, 2003, Davidar *et al.* 2007). Rainfall seasonality and dry season intensity are among the best correlates of species distribution (Bongers *et al.* 1999, Condit *et al.* 2013). In most of the tropical forests, dry season droughts occur very often once or twice per year (Walsh and Newbery 1999), and even in very wet aseasonal tropical forests dry spells of 15 days have been reported to occur at least every other year (Burslem *et al.* 1996, Walsh and Newbery 1999). Plants can therefore be exposed to drought stress with leaf water potential reaching –6.0 MPa (Choat *et al.* 2006) resulting in wilting and increased seedling mortality.

Temperature and light tend to co-vary in tropical forest (Wood *et al.* 2012). As a result it is expected that there will be a gradient in temperature as one moves from a wetter forests to a drier forest. In drier forest there is a higher amount of light especially on the forest floor due to a sparse canopy and deciduousness of a greater percentage of the species. In spite of this possible gradient many tropical forest species have been viewed as being thermally specialised which is a result of an evolved response to less variability in temperature during the course of the year (Janzen 1967). However, it has recently been hypothesised that small changes in temperature affect the distribution of tropical species (Wright *et al.* 2010). There are so far little data to test this hypothesis.

Climate change and tropical forests

The tropics have been traditionally regarded as an area of relative climate stability, but during the past few decades the climate has changed more rapidly than before, and the latest scenarios predict continuation of this pattern in the near future (IPCC 2013). Between 1960 and 1990 air temperatures have increased by 0.26°C per decade over the tropical biome (Malhi &Wright 2004) which is about twice the rate of increase (0.12°C per decade) reported for global temperature for the period 1951–2012 (IPCC 2013). Global warming is also likely to lead to changes in precipitation. A drying trend (more than 4% precipitation decrease per decade) has been reported over the last four decades for West Africa and this was the fastest rate of change reported for tropical forests worldwide (Malhi & Wright 2004). Although there is uncertainty about future changes in rainfall in Africa (Hulme *et al.* 2001), recent predictions for the period 2016-2035 (relative to 1986–2005) based on Representative Concentration Pathway (RCP4.5) scenario indicate a 10% reduction in October–March rainfall for Western Africa (IPCC 2013). For Ghana, General Circulation Models and Simple Models indicate that by 2050 the amount of rainfall may decrease in all ecological zones but most strongly (minus 20%) in the rain forest zone in the south-west of the country (GoG 2011). The increase in temperature as well as the reduction in rainfall is expected to have impacts on the distribution and functioning of tropical forests. Many species are unable to occupy drier sites as a result of their inability to survive drought. Consequently, seasonal patterns of rainfall and drought will be more significant in determining species response to shifts in climate rather than the total quantity of precipitation (Condit 1998). However, higher temperatures may increase vapour pressure deficits, cause stomata to close or increase respiration at the expense of photosynthesis, thus possibly exacerbating effects of changes in rainfall, and having a negative impact on tree growth and forest productivity (Clark *et al.* 2003, Lewis *et al.* 2004, Feeley *et al.* 2007).

For Africa and West Africa vegetation shifts are predicted (Neilson *et al.* 1998) based on the fact that in the late Holocene, less humid condition led to important shifts in the structure and composition of African lowland rainforest (Vincens *et al.* 1999, Ngomanda *et al.* 2007). West African forests are important for the world's biodiversity conservation as for example 22% of forest species in Upper Guinea are restricted to this region (Jongkind & Wieringa, 2004) of which the wet evergreen and dry semi-deciduous forests in Ghana form a part. The forest vegetation in West African is determined by a rainfall gradient ranging from 4000mm to less than 1000 mm (Poorter *et al.* 2004). According to Holmgren *et al.* (2004) the probability of occurrence of 71% of endemic species in this region are related to annual rainfall. Given the high sensitivity of these species to rainfall, shifts in their distribution are highly likely under a drier climate. However, the mechanisms underlying such potential vegetation shifts are generally unknown. Additionally, the potential response of tropical tree species to predicted changes in climate remains poorly understood (Feeley *et al.* 2007, Wright 2010, Corlett, 2011). Understanding species response to temperature and especially drought becomes critical for understanding potential impacts of climate change on the forest ecosystem.

Forest and tree regeneration

Seedling establishment survival and growth play a very important role in the dynamics of the forest as seedling recruitment determines the future population structure of the forest (Schiøtz *et al.* 2006). Additionally, sufficient regeneration is of major importance when utilising forests for timber production. Tree seedling growth and survival in the forest are influenced by light, water availability, temperature, nutrient supply, herbivores and pathogens and other disturbances such as fire and logging (Swaine & Becker 1999). Seedlings are likely to be most sensitive to drought (Marod *et al.* 2002, Gerhardt 1996) because they have shallow root system, which impedes adequate access to deeper soil layers with high water availability (Tyree *et al.* 2003; Engelbrecht *et al.* 2005). In an experiment with seedlings of 15 Ghanaian tree species, drought (water availability) was found to have a stronger effect on seedling mortality than soil fertility (Veenendaal & Swaine, 1998). In another experiment in Barro Colorado Island, mammalian herbivory contributed to the death of 32% of young seedlings that died of drought (Howe 1990). There is also an interaction effect of light and water availability on seedling performance especially, in the understory of the forests. When water is limiting, mortality is increased and growth is reduced at higher light levels especially for shade tolerant species (Brenes-Arguedas *et al.* 2011).

Functional traits and drought adaptations

Plants show many acclimatisation and adaptation responses to environmental factors, especially to drought (Borchert 1998). The growth, survival and reproduction of tropical tree seedlings in any given environment, and their capacity to adapt to changes in that environment depends on the complex interaction of morphological, physiological and phenological traits of each individual species (Garwood 1996). A plant trait is defined as any morphological, physiological or phenological feature that can be measured on an individual, from the cell to whole-organism level, without reference to the environment (Violle *et al.* 2007). A functional trait therefore is any trait which impacts plant fitness indirectly through its effects on growth, reproduction and survival (Violle *et al.* 2007). This thesis focuses on traits that are related to biomass allocation, tissue characteristics and whole-plant morphology and physiology and how these influence plant performance (growth and survival) under drought.

Drought performance has been found to be an important determinant of species distribution with respect to length of dry season, as species with poor drought performance are excluded from drier forests (Engelbrecht, *et al.* 2007). Drought performance is the ability of species to survive low water availability in the field (Kursar *et al.* 2009) whilst being also exposed to other stresses such as changes in pest and nutrients (Tyree *et al.* 2003). Plants have developed three strategies to deal with drought: drought avoidance (ability to shed off leaves at the onset of dry season to reduce water loss), drought delay (ability to capture more water and reduce water loss), and physiological drought tolerance (i.e. the ability of plants to function at low water potential) (Tyree *et al.* 2003, Kursar *et al.* 2009, Poorter & Markesteijn 2008, Markesteijn & Poorter 2009). A trait that is associated with drought avoidance is deciduousness, and traits associated with drought delay include early stomatal closure to reduce water loss and a deep and large root system to increase water uptake. Physiological drought tolerance to low tissue water status is based on physiological traits such as resistance of the xylem to embolism. Two key physiological traits underlying drought tolerance, the lethal water potential (lowest leaf water potential associated with living leaf tissue) and lethal relative water content (the lowest relative water content associated with living leaf tissue), have been shown to correlate strongly with the distribution of tropical tree species along the rainfall gradient (Baltzer *et al.* 2008).

Stem density has also been identified as an important trait for tolerating drought (Markesteijn & Poorter 2009) and is also associated with species position along the rainfall gradient (Maharjan *et al.* 2011). Higher stem density enables plants to resist cavitation (Jacobsen *et al.* 2007, Markesteijn *et al.* 2011, Méndez-Alonzo *et al.* 2012) because of narrow and structurally reinforced vessels that decrease the chance of embolism and reduce vessel implosion (Hacke *et al.* 2006, Jacobsen *et al.* 2007, Lens *et al.* 2013).

Drought tolerance and its trade-off with shade tolerance

Light and water availability co-vary in tropical forest and influence tree species drought performance. Tropical rainforest tree species have been categorised into two key functional groups that represent the extremes of a continuum in species response to the light gradient (Swaine & Whitmore 1988). Shade-tolerant species can germinate, grow and survive in low light, whereas, light-demanding species need a high-light environment for establishment (Agyeman *et al.* 1999, Kyereh *et al.* 1999).

A number of hypotheses postulate a trade-off between shade performance and drought performance. The influential *trade-off* hypothesis predicts a stronger impact of drought on individual species growing in shade than on individual species growing in higher irradiance (Smith & Huston 1989). The hypothesis postulates that shade individuals or shade species have a higher specific leaf area (area of leaf per unit dry mass of leaf) and leaf area ratio (total leaf area per unit plant mass) to enhance light capture in the shade, which comes at the expense of allocation to roots. As a result, shaded plants and shade species should be more sensitive to drought (Smith & Huston 1989). In contrast the *facilitation hypothesis* postulates that drought has a weaker impact on plants in shade, because of lower air temperatures and vapour pressure deficits in shaded microsites (Holmgren *et al.* 1997, 2000, Valladares & Pearcy 1997). A recent alternative hypothesis *(uncoupled hypothesis)* suggests that shade and drought tolerance *vary independently* across forest and shrub species (Sack & Grubb 2002, Sack 2004). This would lead to more niche differentiation as species could compete optimally at any combination of light and water in space and time (Wright 2002). Studies in the temperate region found trade-offs between shade tolerance and drought performance (Niinemets & Valladares, 2006). However, other studies (Sack & Grubb 2002, Sack 2004) in the temperate zone found no trade-off between shade tolerance and drought tolerance, because shade and drought tolerant are controlled by different morphological traits (Sack 2004, Engelbrecht *et al.* 2007a, Markesteijn *et al.* 2011). However these results could be different if the studies would have included physiological traits.

Many studies on seedling regeneration in the tropics have focused on the effect of light. However, there have been few studies (e.g. Burslem 1996, Fisher *et al.* 1991, Veenendaal *et al.* 1996c) on the interaction between light and water and how this influences seedling performance and tree regeneration. These interaction studies have focused on very few species, which makes it difficult to make generalisations. Moreover, very few studies have directly related species shade and drought tolerance to a quantitative measure of the distribution of the species.

In this study, I quantified the position of individual species on the rainfall gradient by using a large inventory data set of 2505 1-ha plots (Hawthorne 1995, 1996) and climatic variables. I in turn investigated the response of a large number (24) of species to drought and light in a controlled experiment. I further evaluated the performance of 23 species in a reciprocal planting experiment in dry and wet forests. By combining the results of controlled and field experiments, with quantitative data on the distribution pattern of the species, this study furthers our understanding on how species respond to environmental conditions and how this is driven by species adaptation and underlying mechanisms. Such information is highly needed as an input for process-based models, to predict the potential impact of climate change and reduced rainfall on forest tree species distribution (Vesk 2013). Knowing species-specific responses to variation in rainfall and seasonality can also help in selecting species to enhance the success of large-scale reforestation efforts (Craven *et al.* 2011).

Research objective and questions

The aim of the study was to determine species responses to drought, and the underlying mechanisms. To achieve this objective four main questions were addressed: (1) What is the relative importance of rainfall and temperature on tree species distribution? (2) How do tree species acclimatise to drought and shade in terms of their physiology, morphology, growth and survival? (3) What morphological and physiological traits determine species drought performance and distribution? (4) How do seedling survival, growth and physiology in the field vary between dry and wet forests, and does drought tolerance and growth determine species distribution along the rainfall gradient?

Thesis outline

This thesis consists of six chapters. The first chapter provides background information on the role of biotic and abiotic factors in the distribution of tropical species. It reviews the different strategies to deal with drought stress, the interaction between light and water in shaping plant performance and the role of functional traits in explaining the performance and distribution of species.

In the second chapter, I used forest inventory data from 2505 1-ha plots systematically distributed across Ghana to analyse the distribution (presence/absence) of 20 important tree species that are used as timber and medicine. I evaluated to what extent species distribution is associated with annual rainfall and temperature, and discuss the consequences of a possible future reduction in rainfall for the distribution of these species.

In the third chapter, I used a controlled cross-factorial greenhouse experiment to evaluate the effect of drought and shade on the performance, allocation, morphology and physiology of 10 Ghanaian tree species. Additionally, I evaluated the relationships between morphological plasticity and growth and drought survival. Finally, to find evidence for the trade-off hypothesis between drought tolerant and shade tolerant, I evaluated the interaction effect of shade and drought on morphological traits and plant performance.

In the fourth chapter, I used the same greenhouse experiment with 24 species to evaluate what morphological and physiological traits are the best predictors of drought survival and species distribution. The dry-down experiment in the controlled environment is important as it helps to isolate other confounding factors (e.g. herbivore and pathogens) that can influence plant traits and performance. Such information gives insight into the mechanisms underlying species drought survival and distribution.

In the fifth chapter, I carried out a reciprocal transplanting experiment in the field. Seedlings of 23 tree species showing contrasting distributions (dry, ubiquitous, moist and wet) were planted in gaps in dry and wet forests in Ghana. I investigated seasonal patterns in environmental conditions, and seedling performance (survival and growth) and physiology over a 2-year period. I related seedling performance to the species distribution along the rainfall gradient.

In the sixth chapter I link the major findings of chapters 2-5. I discuss what biotic factors shape species distribution along the rainfall gradient, the underlying mechanisms and plant strategies (Fig 1.1). Furthermore, I discuss how abiotic factors and plant drought tolerance strategy influence species distribution and what this means for the impact of climate change on tropical forests. I discuss the implication of my findings for forest ecology, management and conservation, and for the selection of species and sites for current reforestation efforts. Finally, I conclude with recommendations for the development of a strategy to mitigate and adapt to climate change impact on forests.

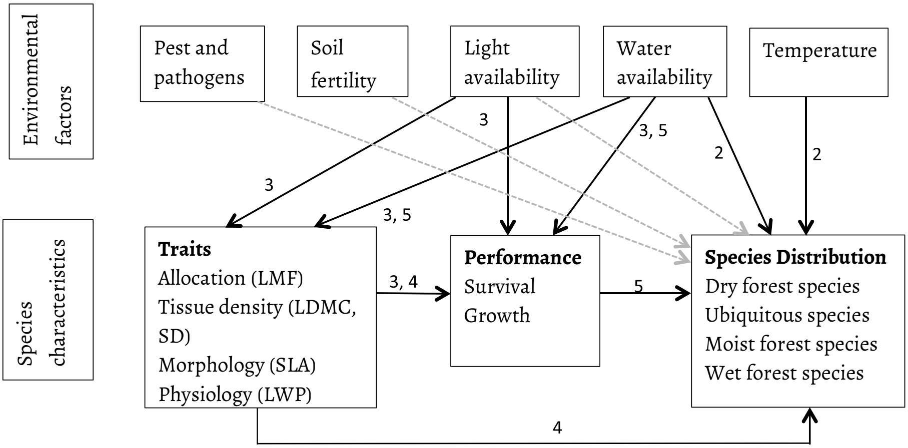


Figure 1.1 Conceptual frame work showing how biotic (pest and pathogens) and abiotic environmental factors (water availability, light availability, temperature and soil fertility) influence tree species distributions. It shows the links between functional traits, species performance (growth and survival) and species distribution. The numbers along the arrows indicate the chapter of the thesis that addresses the specific issue. The dotted arrows are factors that co-shape species distribution but for which result are not presented in this thesis. LMF = leaf mass fraction, LDMC = leaf dry matter content, SD = stem density, SLA = specific leaf area, LWP = leaf water potential. Ubiquitous = occurring in all forest types in Ghana , “dry”, “moist” and “wet” describe wetness. That is dry forest, moist forest and wet forest of Ghana.

Study site

The study was conducted in the tropical lowland forests of Ghana. Ghana’s forest vegetation is classified into seven main forest types namely; Wet Evergreen, Moist Evergreen, Upland Evergreen, Moist semi-deciduous, Dry semi-deciduous, Southern Marginal and South-east Outliers forests (Hall and Swaine, 1976, Fig

1.2). The forests are characterised by a rainfall gradient which varies from < 750 mm to > 2000 mm year^{-1}. Mean annual temperature in the forest zone (1961-2000) ranges from 26.4° C - 27.2 °C. Over the same period mean annual maximum and minimum temperatures in the forest zone range from 29.3-32.0°C and 21.8-23.6 °C respectively (Ghana Meteorological Agency records, 22 synoptic weather stations across Ghana). The wet evergreen type experiences the highest rainfall (>1750 mm per year in some areas and >2000 mm in other areas) and is home to the highest diversity of plants. As a result of the high diversity of plant species trees density is low. Due to the high rainfall the soils are severely leached. The moist semi-deciduous forest experiences rainfall in the range of 1200-1800 mm per year. Most common species in Ghana achieve their highest abundance in this forest type (Hall & Swaine 1981). The elevation is between 150-600 m and soils here are more fertile than the wet evergreen type. The moist evergreen type is intermediate of the wet and the moist type but has higher species diversity than the moist forest and less than 20% of trees here are deciduous. The dry semi-deciduous forest type exists under a wider range of environmental conditions than the other types. Part of it forms a band around the moist type and lies adjacent to the Guinea savannah. Most of the forests under this type receive annual rainfall in the range of 1250-1500 mm (Hall & Swaine 1981). About 20% of the forest area is degraded due to various forms of land use and this together with predicted reduction in rainfall will make the forest more vulnerable to further disturbance such as fire (Hawthorne & Abu-Juam 1995).

Ghanaian forests are generally situated on two main soil types namely oxisols and ochrosols. Oxisols are highly leached, yellowish, very acidic and nutrient poor soils, whereas ochrosols are less leached, reddish, slightly acidic and better supplied with nutrients (Brammer 1962, Hall & Swaine 1981). The wet evergreen forest type is mostly found at the south-western part of Ghana on oxisols, whereas the moist and dry semi-deciduous forest types are situated on ochrosols. The moist evergreen forest type lies on oxisol-ochrosol intergrades. Within the forest zones exists gazetted forest reserves, which have been designated for biodiversity conservation, watershed protection and timber production.

The analysis of the distribution of 20 tree species in relation to rainfall and temperature was conducted using a Ghanaian national forest inventory data summarised by Hawthorne (1995, 1996) and Hawthorne & Abu Juam (1995). The inventory area was located between latitude 4.7°- 8° N and longitudes 3.2° W- 0.6°

E. The inventory covered 127 of the forest reserves which represent most of the forest gradient in Ghana.

The greenhouse experiment (chapters 3 and 4) was conducted at the Council for Scientific and Industrial Research-Forestry Research Institute of Ghana (CSIR-FORIG). The area falls within the moist semi-deciduous forest zone of Ghana with a yearly rainfall of about 1500 mm. The experiment was conducted from August-November 2010 and February –May 2011.

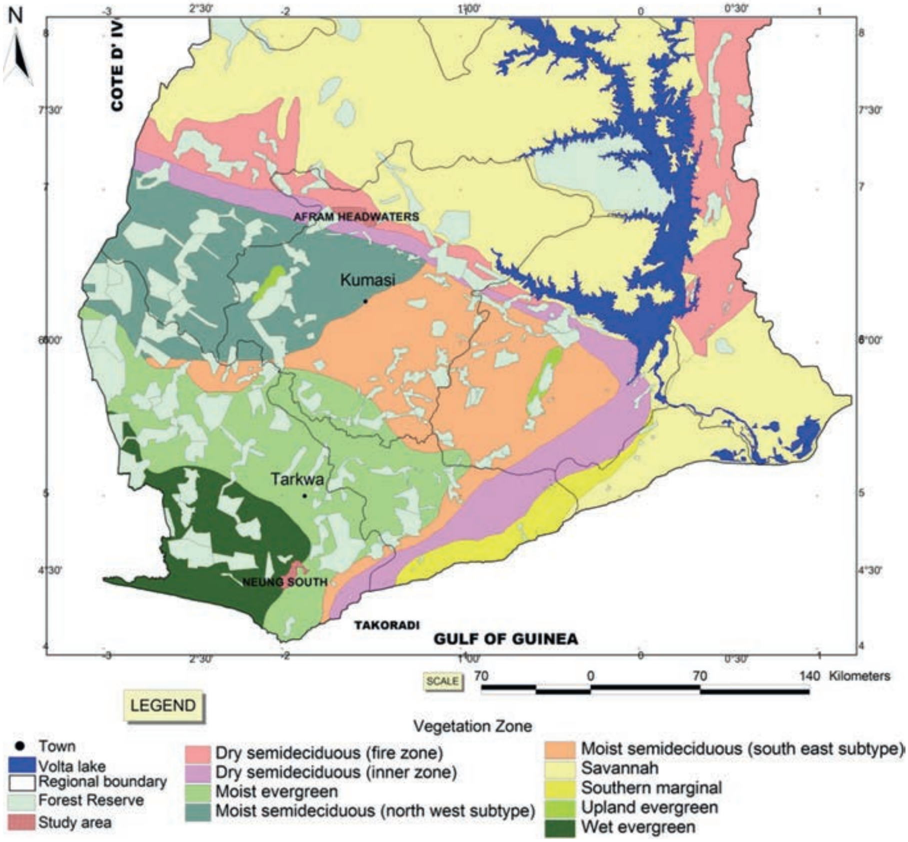
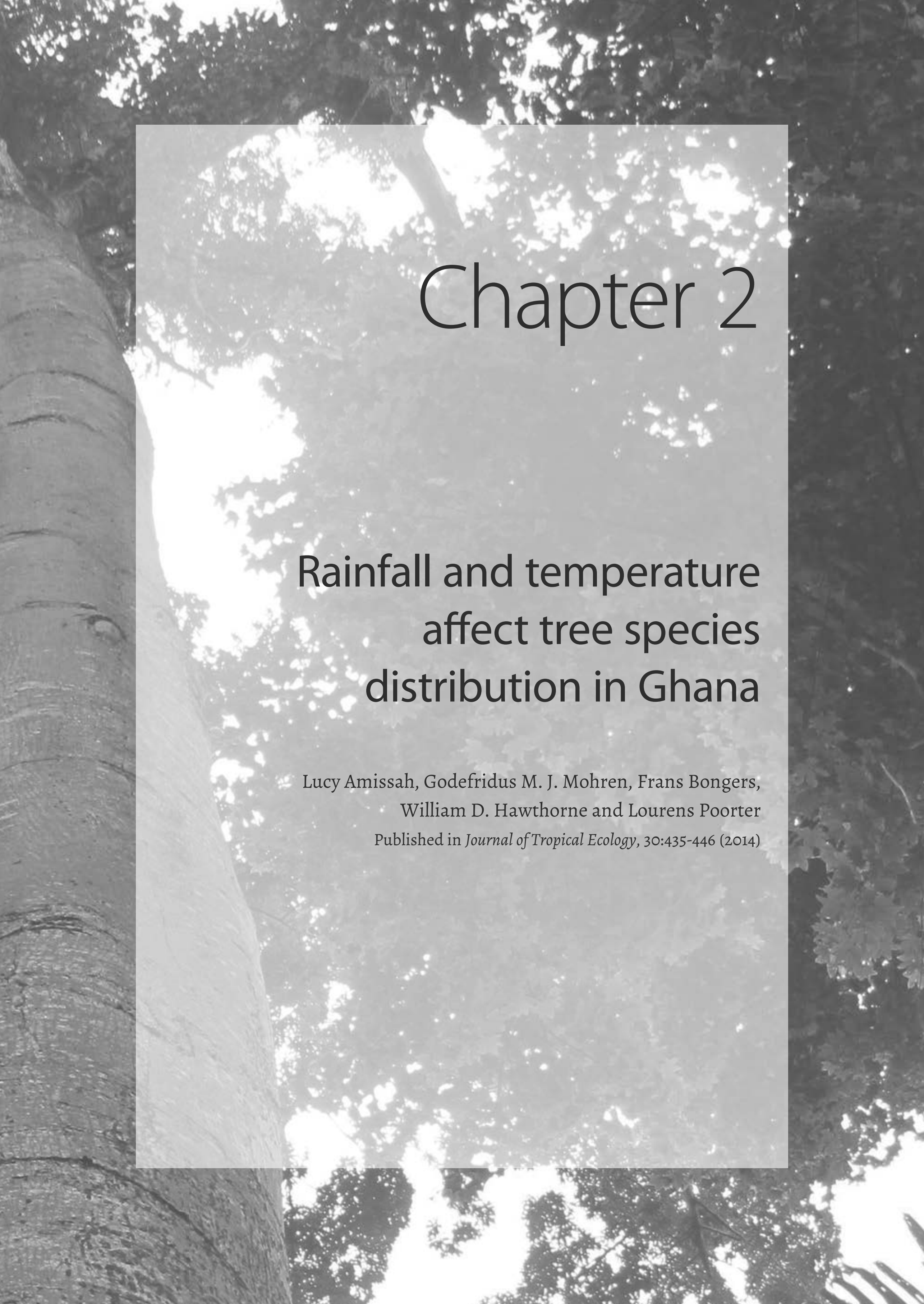


Figure 1.2 Map showing the vegetation zones of Ghana, forest reserves and the study sites (Afram Headwaters and Neung South Forest Reserves).

The field experiment was conducted from June 2011-July 2013 in two forest reserves with contrasting characteristics; the Afram Headwaters Forest Reserve which is a dry forest and Neung South Forest Reserve which is a wet forest (Fig. 1.2). Afram Headwaters Forest Reserve is classified as a dry semi-deciduous forest inner zone subtype (Hall & Swaine 1981). It covers an area of 201 km² and lies on longitude 1°32' W and 1°48' W and latitude 6°45 'N and 7°25 'N. The altitude varies from 274-412 m above sea level. There are few steep slopes in the eastern part. The area in general is a plateau with numerous streams draining it. The Neung south forest reserve is classified as wet evergreen forest (Hall & Swaine 1981). It is located between longitude 1° 55' W and 2° 07' W and latitude 05° 06' N and 5° 11' N. The reserve has an area of 113 km² of which 73 km² is designated as Globally Significant Biodiversity Area (GSBA) because of its relatively high plant species diversity (Forestry Commission 2007).



Chapter 2

Rainfall and temperature affect tree species distribution in Ghana

Lucy Amissah, Godefridus M. J. Mohren, Frans Bongers,
William D. Hawthorne and Lourens Poorter

Published in *Journal of Tropical Ecology*, 30:435-446 (2014)

Abstract

We evaluated the relative importance of annual rainfall, temperature and their seasonality to tree species distribution in Ghana. We used species presence/absence data from 2505 1-ha plots systematically distributed over Ghana's forests. Logistic regression was used to determine species responses to four climatic variables generated from the Worldclim database. The distribution of 95% of 20 species was significantly associated with annual rainfall, 60% with rainfall seasonality, 45% with isothermality and 40% with temperature seasonality. Annual rainfall explained on average most of the variation (17%, range = 0.5%-52%) in species distribution, followed by rainfall seasonality 5% (range = 0.5%-27%), isothermality 4% (range = 0.8%-24%) and temperature seasonality 1% (range = 0.4%-4.5%). Our results suggest that, out of the climatic variables investigated, rainfall is the main factor determining tree species distribution in Ghana; temperature also influences the distribution of a number of species, although it explains much less of the variation. The reduction in annual rainfall that prevailing climate-change scenarios predict for the region will result in a shift in the distribution of most species, whereas the predicted increase in temperature variation is likely to have little effect.

Key Words: climate, distribution, drought, plant-climate interactions, species response curves, temperature, tropical forest

INTRODUCTION

Insight into how individual species respond to resources in tree communities is critical for understanding how environmental factors influence the distribution, abundance and coexistence of tropical tree species (Condit *et al.* 2013). At a large scale, rainfall has been shown to influence species richness (ter Steege *et al.* 2006), composition (Hall & Swaine 1976) and distribution (Bongers *et al.* 1999, Engelbrecht *et al.* 2007, Swaine 1996, Toledo *et al.* 2012), whereas at smaller scales soil fertility, topography and irradiance can affect species distribution (John *et al.* 2007, Veenendaal *et al.* 1996c). Most tropical forests show seasonal variation in rainfall, and species drought performance and physiological drought tolerance have therefore been found to determine the distribution of tropical species (Baltzer *et al.* 2008, Engelbrecht *et al.* 2007).

A number of studies (Hall & Swaine 1976, John *et al.* 2007, Toledo *et al.* 2012) have used composite axes of multivariate environmental gradients and vegetation gradients to analyse species distribution, but the use of such axes does not give insight into how individual species respond to specific environmental factor (Condit *et al.* 2013). For example, several species in Ghana (e.g. *Khaya anthotheca* and *Pericopsis elata)* do not follow the main vegetation gradient that parallels the annual rainfall gradient, and by inference may not follow the rainfall gradient (Hawthorne 1995). Studies that have evaluated the response of tropical tree species to individual environmental gradients have focused on soil nutrients, rainfall and water availability, but far less attention has been paid to the role of temperature. Seasonal variation in temperature is rather minor across most tropical forests, but recent studies suggest that small changes in temperature are likely to affect species distribution patterns (Wright 2010), although there are still few data to support this point. Determination of individual species response curves to a range of climatic variables is imperative to identify the climatic variables that are biologically most relevant to individual plant species, as they can help to predict the possible consequences of climate change for tropical forests (Borchert 1998).

Vegetation structure and composition vary continuously along environmental gradients and theoretical models assume that species show bell-shaped, symmetrical responses to gradients (Gauch & Whittaker 1972) especially when the gradient is long such as the rainfall gradient in Ghana. However, there is growing evidence that many species show asymmetrical response curves to environmental gradients (e.g., Oksanen & Minchin 2002).

In this study, we evaluated the distributions of 20 Ghanaian woody tree species that are economically important (for timber or non-timber products), have contrasting distributions within forest types, and that differ in shade tolerance. We described species distributions using detailed inventory data from 2505 1-ha plots across a steep rainfall gradient (1100-2000 mm y^{-1}) in Ghana. We determined the influence of annual rainfall, temperature, and their seasonality on species presence/absence. The size of this study (2505 plots) is an order of magnitude larger than has been studied so far (e.g. 220 plots by Toledo *et al.* 2012, 72 plots by Condit *et al.* 2013). Two questions were addressed: First, what is the relative importance of annual rainfall, temperature and their seasonality for species distribution? We hypothesized that annual rainfall, and especially rainfall seasonality will be stronger drivers of species distribution than temperature (seasonality). Second, what is the shape of species response curves along these environmental gradients? We hypothesized that unimodal response curves will be more associated with rainfall gradient than temperature gradient because under relatively benign conditions environmental resources (such as water) are more important in shaping species responses than environmental conditions such as temperature.

MATERIALS AND METHODS

Study site

The study was based on Ghanaian national forest inventory data summarised by Hawthorne (1995, 1996) and Hawthorne & Abu-Juam (1995). The study area was located between latitude 4.7°-8.0°N and longitudes 3.2° E-0.6° W. Based on floristic composition, the forest vegetation of Ghana has been classified into seven main forest types: wet evergreen, moist evergreen, upland evergreen, moist semi-deciduous, dry semi-deciduous, southern marginal and south-east outlier forests (Hall & Swaine 1976). The forests are characterised by a rainfall gradient which varies from < 750 to > 2000 mm y^{-1}. Mean annual temperature in the forest zone (1961-2000) ranges from 26.4° C-27.2° C. Over the same period mean annual maximum and minimum temperatures in the forest zone range from 29.3°C-32.0°C and 21.8°C-23.6°C respectively (Ghana Meteorological Agency records, 22 synoptic weather stations across Ghana). Mean monthly maximum temperature in the hottest month (February or March) is 31°C -33°C and mean monthly minimum temperature of the coldest month (August) is 19°C -21°C (Hall & Swaine 1981). Annual rainfall (in the period 1961-2000) ranges from 1300 mm to 2032 mm in the forest zone (Ghana Meteorological Agency records, 22 synoptic weather stations across Ghana). In a recent analysis of data from 77 weather stations distributed all over Ghana, mean annual rainfall for the period 1981- 2010 ranged from 1000 mm to 1900 mm in the forest zone (Logah *et al.* 2013). Means, ranges and ratios (maximum over minimum) of the four variables (Worldclim data) for the plots used in the analysis are provided in Appendix 1.

Forest inventory data

Ghana has a total forest cover of 7,665,900 ha (FAO 2010) including 214 forest reserves designated for timber production, watershed protection and biodiversity conservation. Within these forest reserves, a systematic forest inventory was carried out between 1986 and 1991 (Hawthorne 1995, 1996, Hawthorne & Abu-Juam 1995). The inventory covered 127 of the forest reserves which represent most of the forest gradient in Ghana. These reserves were sampled systematically in a 2 × 2-km grid with 1-ha plots at the grid intersections. In total, 2505 1-ha plots were inventoried with a nested design. All trees ≥ 30 cm diameter at breast height (dbh) were identified over the entire plot. Trees 10-30 cm dbh were identified in 0.1-ha subplots, and trees 5-10 cm dbh were identified in 0.05-ha subplots. For this analysis, species abundance data were converted into presence and absence data. Presence and absence data were preferred over abundance data because differences in species abundances respond to a wide range of processes such as competition, and recovery from past disturbances (Toledo *et al.* 2012). We selected 20 species based on their economic importance for society (for timber or as a source of medicine), distribution in contrasting forest types and representation of different guilds (Table 1). The forest types are related to several factors (e.g. soils, topography, rainfall and temperature) and these together determine the actual water availability over the year (Swaine 1996). We recognise that the selection is partly based on rainfall but emphasize that this is only one factor among several (Table 1). Therefore we are confident this is not interfering strongly with our main results. Of the 20 species seven are pioneers (species require gaps for seedling establishment and growth); seven are non-pioneer light-demanders (seedlings are present in the shaded understorey but require light environment to reach adult size); and six are shade tolerant (species that are able to establish and continue to grow in forest shade; Hawthorne 1995).

Table 1. The 20 Ghanaian woody species studied, their family, ecological guild and preference for a different forest type based on Hall & Swaine (1981), Hawthorne (1995), Hawthorne & Jongkind (2006) and Hawthorne & Ntim Gyakari (2006). NPLD = Non-pioneer light demander, SB = Shade bearer, P = Pioneer, Abbrev = Abbreviation.

Species	Abbrev	Family	Forest type	Guild
Heritiera utilis Sprague	Hu	Sterculiaceae	Wet	NPLD
Cynometra ananta Hutch. and Dalz.	Ca	Caesalpiniaceae	Wet	SB
Diospyros sanza-minika A. Chev.	Ds	Ebenaceae	Wet	SB
Pentadesma butyracea Sabine	Pb	Caesalpiniaceae	Wet	SB
Entandrophragma angolense (Welw). DC	Ea	Meliaceae	Moist	NPLD
Turraeanthus africanus (Welw. ex C.DC.) Peller	Ta	Meliaceae	Moist	SB
Petersianthus macrocarpus (Beauv.) Liben	Pm	Lecythidaceae	Moist	P
Piptadeniastrum africanum (Hook.f.) Brenan	Pa	Mimosaceae	Moist	NPLD
Ricinodendron heudelotii (Baill.) Pierre ex Pax	Rh	Euphorbiaceae	Dry	P
Newbouldia laevis (P.Beauv.) Seeman ex Bureau	Nl	Bignoniaceae	Dry	P
Mansonia altissima (A.Chev.) A.Chev.	Ma	Sterculiaceae	Dry	NPLD
Nesogordonia papaverifera (A.Chev.) R.Capuron	Np	Sterculiaceae	Dry	SB
Ceiba pentandra (Linn.) Gaertn.	Cp	Bombacaceae	Dry	P
Celtis adolfi-friderici Engl.	Ce	Ulmaceae	Dry	P
Albizia zygia (DC.) J.F. Macbr.	Az	Mimosaceae	Dry	NPLD
Pericopsis elata (Harms) Van Meeuwen	Pe	Papilionaceae	Dry	NPLD
Antiaris toxicaria Leschenault	At	Moraceae	Ubiquitous	NPLD
Strombosia pustulata J.Leonard	Sp	Olacaceae	Ubiquitous	SB
Terminalia ivorensis A.Chev.	Ti	Combretaceae	Ubiquitous	P
Terminalia superba Engl. & Diels	Ts	Combretaceae	Ubiquitous	P

Climate data

Nineteen climatic variables were obtained from the Worlclim data base (Hijmans *et al.* 2005). The data were derived from a compilation of monthly averages of climatic variables measured from a large number of weather stations across the globe, mostly between the periods of 1950-2000 (Hijmans *et al.* 2005). These data were interpolated using ANNUSPLIN to create a global climate data set meaningful for ecological analysis. The dataset has a 1-km resolution and consists of 19 climatic variables. For details see Hijmans *et al.* (2005). We used plot coordinates and in some cases forest reserve coordinates to estimate the values of each of the 19 climatic variables for the study locations. We consider the Wordclim data to be of sufficient resolution for our study. Fauset *et al.* (2012) have shown that habitat scores on the ordination axis 1 of Hall & Swaine (1976, 1981) and Hawthorne & Abu-Juam (1995) are strongly correlated with precipitation data from the Worldclim data. This same axis is also correlated with rainfall data (data from 5 y prior to 1963) from 170 weather stations in Ghana used in the classification of forest types by Hall & Swaine (1976). In the Worldclim database variation in the density of climatic stations was taken into account in the generation of the bioclimatic variables (details in Hijmans *et al.* 2005). Our plots were located inside forest reserves and their microclimate is relatively less disturbed, although past disturbance may have led to increased dryness of the forest and for example to an increase in the presence of light-demanding species.

Selection of climatic variables

A principal component analysis (PCA) (Appendix 2) was conducted to evaluate how all 19 climatic variables were associated for the 2505 plots. The first two PCA axes explained 81% of the variation. We selected four climatic variables that described the two main axis of climatic variation and that were relatively independent from each other; annual rainfall and rainfall seasonality (the coefficient of variation of mean monthly rainfall, in %), temperature seasonality (calculated as standard deviation of mean monthly temperature × 100, in °C), and isothermality (the ratio of mean diurnal temperature range and annual temperature range × 100, in %). An isothermality value of 100 represents a site where the diurnal temperature range is equivalent to the annual temperature range. Values less than 100 indicate a smaller level of diurnal temperature variability (mean of monthly (maximum - minimum temperature)) relative to the temperature variability in a year (maximum temperature of the warmest month - minimum temperature of the coldest month). The selection of the four variables was also based on the fact that they reflected a resource (rainfall) and an important condition (temperature) that physiologically affects the growth of plants (Pausas & Austin 2001),and are predicted to change with climate change. Seasonality may represent a bottleneck for plant performance (Clark *et al.* 2010). Isothermality has been shown to influence plant height growth across latitudes though the relationship is weak (Moles *et al.* 2009). Temperature seasonality is important for species growth and hence for their distribution because most annual net primary production of trees in seasonal forests is concentrated in the months with high rainfall and growth is likely to be most sensitive to temperature variability during this time of the year (Vlam et al. 2014). All four variables were moderately to highly correlated with one of the first two PCA axes. The first axis of the PCA explained 46% of the variation and showed a strong Pearson correlation with annual rainfall ($r = 0.93$), temperature seasonality ($r = 0.66$) and isothermality ($r = 0.73$). Rainfall seasonality also was moderately correlated with the second axis ($r = 0.50$) that explained 35% of the variation. We tested for multicollinearity among the four variables using collinearity statistics. The variance inflation factor was < 3 indicating that all four variables could be included in a regression analysis (Zuur *et al.* 2010). Correlations among the four variables are shown in Appendix 3.

Species response to climatic variables

For each of the species, we conducted a forward multiple logistic regression analysis of presence/absence on the four climatic variables and their quadratic terms. To be able to construct bell-shaped responses both the simple and quadratic terms for each climatic variable were included. We also included interaction terms but the interactions contributed little to the variation (data not shown). For each species the regression model with the lowest deviance (-2 log likelihood) and highest Nagelkerke R^2 was selected (Field 2009). Area under the curve (AUC) of a receiver operating characteristic curve (ROC) (Metz 1978) was used to measure the overall model accuracy (Pearce & Ferrier 2000). We interpreted AUC using the scale proposed by Swets (1988): good = AUC > 0.9; useful = 0.9 > AUC > 0.7 and poor AUC < 0.7. The partial variation contributed by each environmental variable was calculated as the increase in variation when the variable was included in the model. Parameters (Appendix 4) derived from the species-specific regression models were used to calculate the probability of occurrence for each species for all four environmental variables using the formula: $P = 1/ (1 + \mathrm{Exp} (- b_0 - b_1 X_{1-} - b_2 X_1^2 \ldots\ldots\ldots\ldots - b_7 X_4 - b_8 X_4^2))$, where P = probability of occurrence, Exp = exponential, b_0 = a constant, X_{1-4} = the four bioclimatic variables used, b_1-b_8 = coefficients for the four bioclimatic variables and their quadratic terms.

We constructed the response curves for each species against the individual climatic variables using the calculated probabilities, while keeping the other three climatic factors constant. When we kept the other three environmental variables constant, we used their mean values across all 2505 plots in Ghana. Using constant values for the other variables is the only way to directly compare the response curves of different species to an individual climatic variable. We acknowledge that individual species may have their peak occurrence in different parts of the climate space for the other three climatic variables than the mean values for Ghana that we used, which may lead to over- or underestimations of the responses at some part of the climatic gradient for a particular species. The mean values used were 1514 mm y^{-1} for annual rainfall, 53% (coefficient of variation) for rainfall seasonality, 72% for isothermality and 1028°C for temperature seasonality (temperature seasonality being calculated as standard deviation of mean monthly temperature ×100). The temperature data were in units of °C ×10. Hence this means that in normal degrees the average temperature seasonality for the plots is 1.028°C. Species rainfall optimum (R_{opt}) and range (R_{range}) were derived from the species response curves. Rainfall optimum was the value at which species occurrence reached the maximum (ecological optimum). R_{range} was the range of rainfall conditions under which the species occur computed as the difference between the minimum rainfall (rainfall at the 10th percentile) and the maximum rainfall (rainfall at the 90th percentile) (Maharjan *et al.* 2011). All statistical analyses were conducted using Predictive Analytics Software (PASW) statistics for windows version 18.0 (SPSS Incorporated, Chicago, Illinois).

RESULTS

Relative importance of climatic variables for species distribution

Species showed different responses to the four climatic variables studied. Most of the selected regression models (75%) had AUC > 0.7 (Appendix 4) indicating that the models are useful for predicting the occurrence of species using the four climatic variables and presence-absence data. Most of the 20 woody species (95%) showed a significant response to rainfall, followed by rainfall seasonality (60%), isothermality (45%) and temperature seasonality (40%). The logistic regression models explained on average 28% (range = 3%-60% across species) of the variation in species occurrence. On average, 17% (range = 0.8%-52%) of the variation in species occurrence was explained by annual rainfall, 5% (range = 0.5%-27.5%) by rainfall seasonality, 4% (range = 0.8%- 24%) by isothermality and 1% (range = 0.4%-4.5%) by temperature seasonality. For 12 of the 20 species annual rainfall explained, amongst the four factors studied, most of the variation in occurrence (Figure 1). Examples of species affected by annual rainfall are: *Heritiera utilis* and *Pentadesma butyracea*, which are typical wet-forest species; *Mansonia altissima*, which is a typical dry-forest species; and *Terminalia superba,* which is found in all main (wet, moist and dry) forest types in Ghana (Figure 1 & 2). For six of the species rainfall seasonality explained most of the variation of the four factors studied and these were mostly species with peak occurrence in moist forests such as *Entandrophragma angolense* and *Turraeanthus africanus* (Figure 1 & 2). For two of the species (*Strombosia pustulata* and *Piptadeniastrum africanum*), isothermality explained most of the variation in occurrence with reference to the four factors studied. Temperature seasonality did not explain the most (of four factors studied) important variation in the occurrence for any of the twenty species studied (Figure 1).

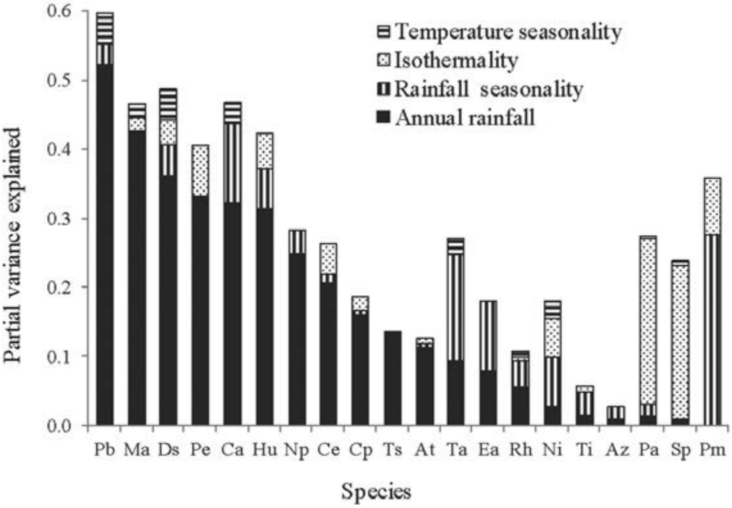


Figure 1. Bar graph displaying variation in species occurrence explained by four climatic variables in multiple logistic regression models for 20 Ghanaian woody tree species. Climatic variables included are: RAN = annual rainfall, RSEAS = rainfall seasonality, ISO = Isothermality, TSEAS = Temperature seasonality. The species are ordered based on the variation explained by annual rainfall. At = *Antiaris toxicaria,* Az = *Albizia zygia,* Ca = *Cynometra ananta,* Ce = *Celtis adolfi-friderici,* Cp = *Ceiba pentandra, Ds = Diospyros sanza-minika,* Ea = *Entandrophragma angolense,* Hu = *Heritiera utilis,* Ma = *Mansonia altissima,* Ni = *Newbouldia laevis,* Np = *Nesogordonia papaverifera,* Pa = *Piptadeniastrum africanum,* Pb = *Pentadesma butyracea,* Pe = *Pericopsis elata,* Pm = *Petersianthus macrocarpus,* Rh = *Ricinodendron heudelotii,* Sp = *Strombosia pustulata,* Ta = *Turraeanthus africanus,* Ti = *Terminalia ivorensis,* Ts = *Terminalia superba.*

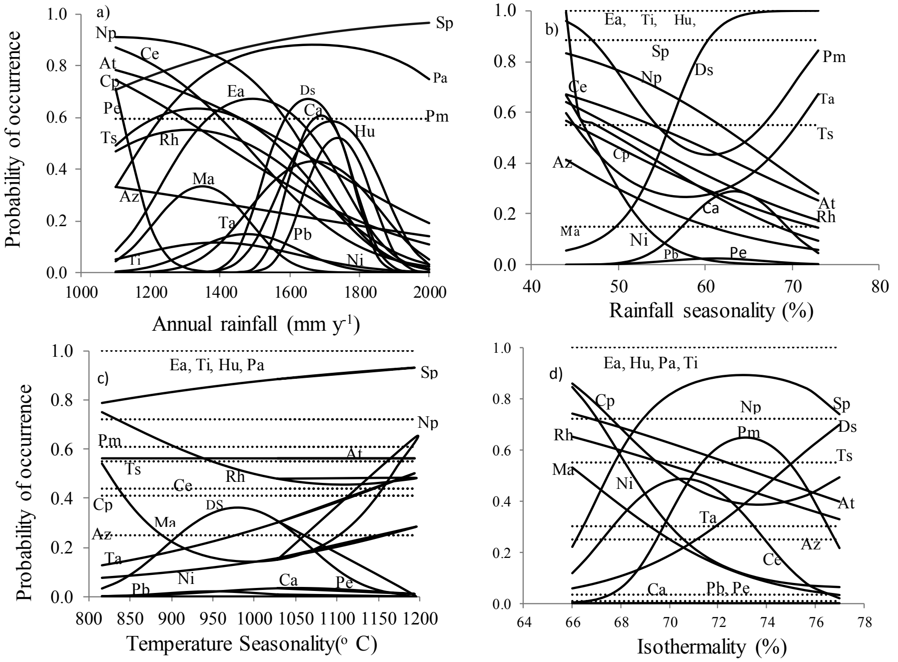


Figure 2. Species response curves showing the probability of occurrence of 20 tropical woody tree species of Ghana in relation to annual rainfall, rainfall seasonality, isothermality and temperature seasonality. Curves give the results of fitted logistic regression models (Appendix 4). The temperature data were in units of °C ×10. Hence temperature seasonality values have been multiplied by 1000. At = *Antiaris toxicaria*, Az = *Albizia zygia*, Ca = *Cynometra ananta*, Ce = *Celtis adolfi-friderici*, Cp = *Ceiba pentandra*, *Ds = Diospyros sanza-minika*, Ea = *Entandrophragma angolense*, Hu = *Heritiera utilis*, Ma = *Mansonia altissima*, Ni = *Newbouldia laevis*, Np = *Nesogordonia papaverifera*, Pa = *Piptadeniastrum africanum*, Pb = *Pentadesma butyracea*, Pe = *Pericopsis elata*, Pm = *Petersianthus macrocarpus*, Rh = *Ricinodendron heudelotii*, Sp = *Strombosia pustulata*, Ta = *Turraeanthus africanus*, Ti = *Terminalia ivorensis*, Ts = *Terminalia superba*. Annual rainfall (a), rainfall seasonality (coefficient of variation) (b), temperature seasonality (calculated as standard deviation of mean monthly temperature × 100) (c), and isothermality (ratio of mean diurnal temperature range and annual temperature range × 100) (d).

Species response to climatic variables

Species showed different response curve types to the four climatic variables studied: unimodal response (Figure 3a), decreasing response (Figure 3b), increasing response (Figure 3c), and flat response, indicating no response. On average 31% (25 of 80) of the response curves were unimodal and such responses were mostly found with respect to the rainfall gradient (12 out of 20 species) and least with respect to isothermality (4 of 20 species). Decreasing response was mostly found with respect to rainfall seasonality (7 of 20 species) and least with respect to isothermality (4 of 20 species). Increasing response was mostly associated with temperature seasonality (3 of 20) and least with rainfall (1 of 20 species). Flat response was mostly associated with temperature seasonality (12 of 20 species) and isothermality (11 of 20 species) (Table 2). Examples of species that showed different response curves are *Diospyros sanza-minika,* which showed a unimodal response to annual rainfall (Figure 2a) but an increasing response to rainfall seasonality and isothermality (Figure 2b,d). *Strombosia pustulata* (Sp) showed an increasing response curve to annual rainfall (Figure 2a) but unimodal response to isothermality (Figure 2d).

Table 2. Number of Ghanaian forest tree species (n = 20) that show different types of response curves, in response to four climatic factors

	Response curve shape			
Climatic factors	Unimodal	Increasing	Decreasing	No response
Annual rainfall	12	1	6	1
Rainfall seasonality	4	1	7	8
Isothermality	4	1	4	11
Temperature seasonality	5	3	0	12

DISCUSSION

We analysed the environmental response curves of 20 important Ghanaian timber species and determined the relative importance of rainfall and temperature to their distribution. Species showed differential responses to the climatic variables but the distributions of most species was strongly influenced by rainfall than by temperature.

Importance of annual rainfall, temperature and their seasonality for species distribution

Rainfall. - This study focused on the relative importance of annual rainfall and its seasonality, temperature seasonality and isothermality for species occurrence and tested the hypothesis that most of the species will respond to annual rainfall and especially rainfall seasonality. We found that nearly all (95%) species were

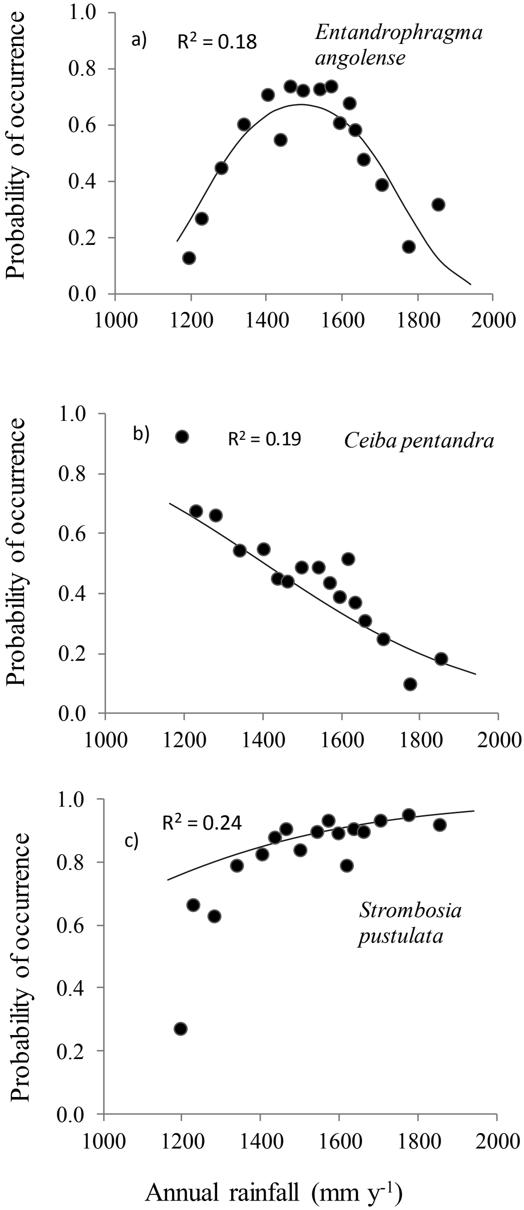


Figure 3. Examples of different species response curves of three of 20 Ghanaian woody tree species to annual rainfall. Species responses (in terms of probability of occurrence) are fitted with logistic regression models. Regression lines show the predicted occurrence in relation to rainfall, while the three other climatic factors (rainfall seasonality, temperature seasonality and isothermality) are kept constant. Dots show the average observed probability of occurrence for rainfall class intervals of 150 plots. To make sure that each rainfall class contained 150 plots, the rainfall classes had variable widths. Unimodal response (a), decreasing response (b) and increasing response (c).

significantly affected by annual rainfall and that annual rainfall explained more (on average 17%) of the variation in species occurrence than the other three factors evaluated (Figure 2). Other studies also found that rainfall was the main driver of large-scale distribution patterns of tropical plant and tree species (Bongers *et al.* 1999, Holmgren & Poorter 2007, Maharjan *et al.* 2011, Toledo *et al.* 2011, 2012). It is surprising that rainfall seasonality explained only 5% of the variation contrary to widely held view that it strongly influences species distribution (Borchert 1998, Kato *et al.* 2000). In a recent study, dry-season intensity was found to be among the main drivers of individual species distribution in Panama (Condit *et al.* 2013). The, at first sight, low percentage variation explained by annual rainfall may have resulted from the small plot size (1- ha) used. The smaller plot size, however, allowed more replicates, and thus a higher statistical power to detect independent variation of various climatic variables affecting the distribution of the species.

Recently, Fauset *et al.* (2012) evaluated the effects of drought on changes in plants functional composition and biomass over a twenty-year period in a variety of forest types in Ghana. They found that, during this period wet-forest evergreen and subcanopy shade-tolerant species decreased in abundance, whereas dry-forest deciduous and canopy species increased in abundance. It is possible that these changes are not only driven by an increase in drought, but also by general increasing levels of disturbance in the forest zone of Ghana over the sampled period. Drier climate coupled with other human activities may result in incidence of fire which leads to further changes in forest composition. Experimental studies (field: Engelbrecht *et al.* 2007, Nepstad *et al.* 2007; greenhouse: Deines *et al.* 2011) showed that seasonal drought has a strong effect on growth and survival of individual tree species, and that drought tolerance is a good predictor of species distribution along the rainfall gradient (Baltzer *et al.* 2008, Engelbrecht *et al.* 2007, Sterck *et al.* in press). Repeated incidental (El Niño) drought also resulted in high mortality of especially trees with low wood density in the Amazon forest (Phillips *et al.* 2010). Additionally, in an Amazonian forest an experimental drought caused a rapid and strong decline in above-ground wood production (Brando *et al.* 2008). In combination, these studies suggest that species drought tolerance is a major determinant explaining species distribution along the rainfall gradient. However, other associated factors such as soil fertility, herbivory and pathogens, and perhaps most significantly, natural and human-induced disturbances such as forest fire, large wind blows and selective logging, can also co-influence species distribution along the rainfall gradient. Disturbance (and density of light-demanding species) also increases with dryness of forest type (Hawthorne 1996). In addition, dispersal limitation may also influence the distribution of species (Duncan *et al.* 2009). In general, soil fertility declines with increasing rainfall in Ghana and Panama (Brenes-Arguedas *et al.* 2008, Swaine 1996, Veenendaal & Swaine 1998), probably because soils in wetter areas are more leached as has been shown for Ghana (Swaine 1996). Controlled experiments that evaluated species growth responses to different wet-, moist- and dry-forest soils in Ghana (L. Amissah *et al.* unpubl. data, Veenendaal *et al.* 1996c) found that the growth of very few species was significantly affected by these soil differences. Planted seedlings in Panama showed a higher overall growth in soils from the drier part of the Isthmus than in soils from the wetter part. Insect herbivore damage and pathogen mortality were more associated with wet forest than dry forest in Panama, suggesting an increasing pest pressure along the rainfall gradient (Brenes-Arguedas *et al.* 2009). However, no significant differences in pest attack levels of wet-forest species and dry-forest species were found. Brenes-Arguedas *et al.* (2009) concluded therefore, that seasonal drought was a stronger determinant of species distribution than pests.

Although the projection of future climate for West Africa is not unequivocal (Christensen *et al.* 2007), Sheffield & Wood (2008) found several IPCC models (IPCC-Assessment Report 4) predicting a reduction in precipitation and increased frequency in long-term soil drought for some subtropical and tropical regions, including West Africa. Furthermore, the precipitation trend in West Africa shows reduction in rainfall (Malhi & Wright 2004) and increasing seasonality (Borchert 1998). Annual rainfall over the past two decades in some forest types in Ghana shows a 22.8% reduction in dry-season rainfall compared with pre-1970 levels (Fauset *et al.* 2012). Additionally, rainfall is predicted to be reduced by 20% in 2050 in Ghana (Government of Ghana 2011). Most forest species are likely to shift their distribution in response to these trends and predictions. In particular for Ghana the distribution of species such as *Heritiera utilis* and *Pentadesma butyracea* that are sensitive to experimental drought (L. Amissah unpubl. data) may shift towards currently wetter forest areas in the south-west of the country.

Temperature. - Isothermality co-explained the distribution of only 10% of the species. *Mansonia altissima* and *Newbouldia laevis,* for instance, showed steep decline in response to an increase in isothermality suggesting that the probability of occurrence of the species may be reduced with larger temperature variability within an average month relative to the year. This seems to contrast sharply with the results from a study in lowland Bolivia, where 72% of the 100 studied species showed a significant response to temperature (Toledo *et al.* 2012). Temperature may have an indirect effect on plant growth. Short-term leaf-level measurements in a number of tropical forest regions showed that net carbon assimilation declines with an increase in daytime temperatures (Doughty & Goulden 2008). Similarly, eddy-flux towers in Brazil and Costa Rica showed a reduced net carbon uptake in the warmest daytime period (Doughty & Goulden 2008, Goulden *et al.* 2004, Loescher *et al.* 2003). Field studies in tropical forests in Costa Rica, Malaysia and Panama also showed negative correlation between tree growth and temperature (Clark *et al.* 2003, Feeley *et al.* 2007). In many countries (like Ghana) where seasonal variability in temperature is large compared to daily variation, predicted increases in temperature may affect the distribution of limited number of species. However, in areas with larger temperature variation, such as the southern edge of the Amazon where cold winds from Patagonia penetrate for short spells, increases in temperature are likely to shift the distribution of more species (Toledo *et al.* 2012).

Shapes of species response curves to environmental gradients

We hypothesised that unimodal response curves will be more often found in relation to the annual rainfall gradient than to the temperature gradient, because under relatively benign conditions, environmental resources (such as water) are more important in shaping species responses than environmental conditions such as temperature. Most species (60%) indeed showed a unimodal response to rainfall, whereas 30% of the species showed decreased and 5% increased occurrence with rainfall across Ghana. In contrast, only 20%-25% of the species exhibited a unimodal response curve to isothermality and temperature seasonality. This could have been attributed to effects of shorter gradient length for temperature, but in our study this was not the case: in fact the gradients were similarly long with 1.5-fold variation for temperature and 1.7-fold variation for rainfall (Appendix 1). Other studies on tropical tree species found a similar or lower number of unimodal response curves; 56% of the studied species along a rainfall gradient in West Africa (Maharjan *et al.* 2011), 42% of the species along a soil-fertility gradient in North-West Amazonia (Duque 2004), and 25% and 10% along a rainfall and temperature gradient respectively in Bolivia (Toledo *et al.*

2012). We acknowledge that these results are not directly comparable as they are also dependent on the species number and selection criteria and on the length and the type of the gradient used.

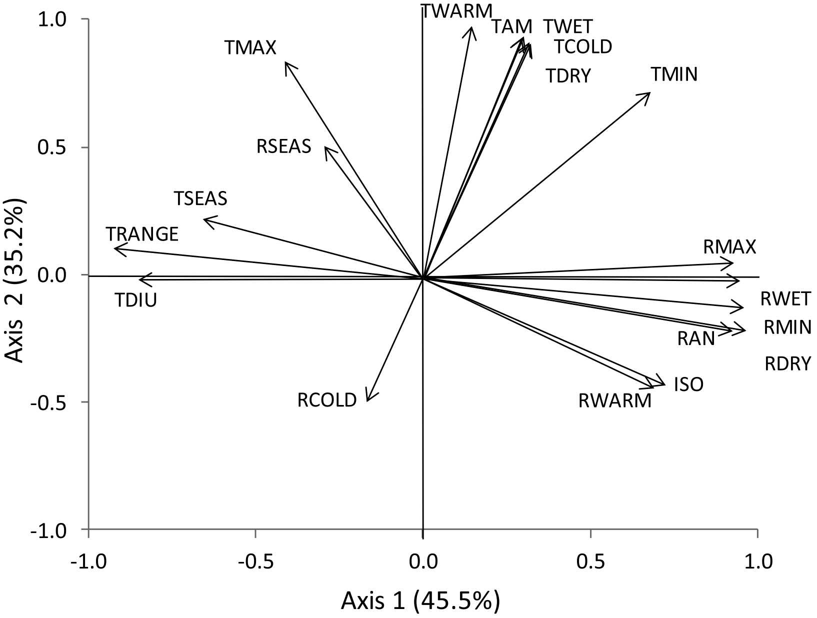
The shape of a species response curve is determined by the length of the gradient and species-specific properties such as tolerance and the position of the optimum (Austin & Smith 1989, Rydgren *et al*. 2003). Generally if the gradient is long, unimodal curves are expected (Gauch & Whittaker 1972, Oksanen & Minchin 2002), but if the optimum of the species is close or beyond the extreme end of the gradient truncated curves are expected (Rydgren *et al*. 2003, ter Braak & Looman 1986). Few unimodal response curves were found for temperature seasonality and isothermality and 55%-60% of the species showed no response. Other environmental factors may drive the shape of the response curve for these species (Austin & Gaywood 1994, Duque 2004), overruling temperature seasonality and isothermality. In sum, this study shows that annual rainfall and seasonality are the man climatic factors influencing distribution of individual tree species in Ghana, though temperature influences the distribution of some species. Predicted increases in frequency and severity of drought may cause shifts in the distribution of species that occur at the wetter side of the rainfall gradient.

ACKNOWLEDGEMENTS

LA was supported by a grant from Wageningen University and the Netherlands Fellowship Programme (NUFFIC). We thank Dr. Mike Swaine for providing advice on species selection and allowing us to use his data base of species and their ordination scores, and an anonymous reviewer for their helpful comments

Appendix 1: Mean, range (minimum and maximum) and ratio (maximum divided by the minimum) of climatic variables of 2505 forest plots of Ghana. The mean, range and ratio are based on climatic data obtained from the Worldclim data base (Hijmans *et al*. 2005).

Parameters	Mean	Range	Ratio
Annual rainfall (mm)	1510	1160-1940	1.66
Rainfall seasonality (%)	53	44-73	1.37
Temperature seasonality (°C)	1030	816-1210	1.48
Isothermality (%)	72	66-77	1.16



Appendix 2. Principal Components Analysis (PCA) on 19 climatic variables for 2505 forest sites in Ghana. The first and second axes explain respectively 46% and 35% of the variation. RAN = annual precipitation TSEAS = temperature seasonality, RSEAS = precipitation seasonality, ISO = isothermality, TAM = annual mean temperature, TDIU = temperature mean diurnal range, TMAX = max temperature of warmest month, TMIN = min temperature of coldest month, TRANGE = temperature annual range, TWET = mean temperature of wettest quarter, TDRY = mean temperature of driest quarter, TWARM = mean temperature of warmest quarter, TCOLD = mean temperature of coldest quarter, RMAX = precipitation of wettest month, RMIN = precipitation of driest month, RWET = precipitation of wettest quarter, RDRY = precipitation of driest quarter, RWARM = precipitation of warmest quarter, RCOLD = precipitation of coldest quarter. The climatic variables were obtained from the Worldclim data base (Hijmans *et al*. 2005).

Appendix 3: Pearson correlations among annual rainfall (RAN), rainfall seasonality (RSEAS), temperature seasonality (TSEAS) and isothermally (ISO) and their P values. ***P ≤ 0.001, n = 2505. The four climatic variables are for 2505 1-ha forest plots in Ghana. The climatic variables were obtained from the Worldclim data base (Hijmans *et al.* 2005).

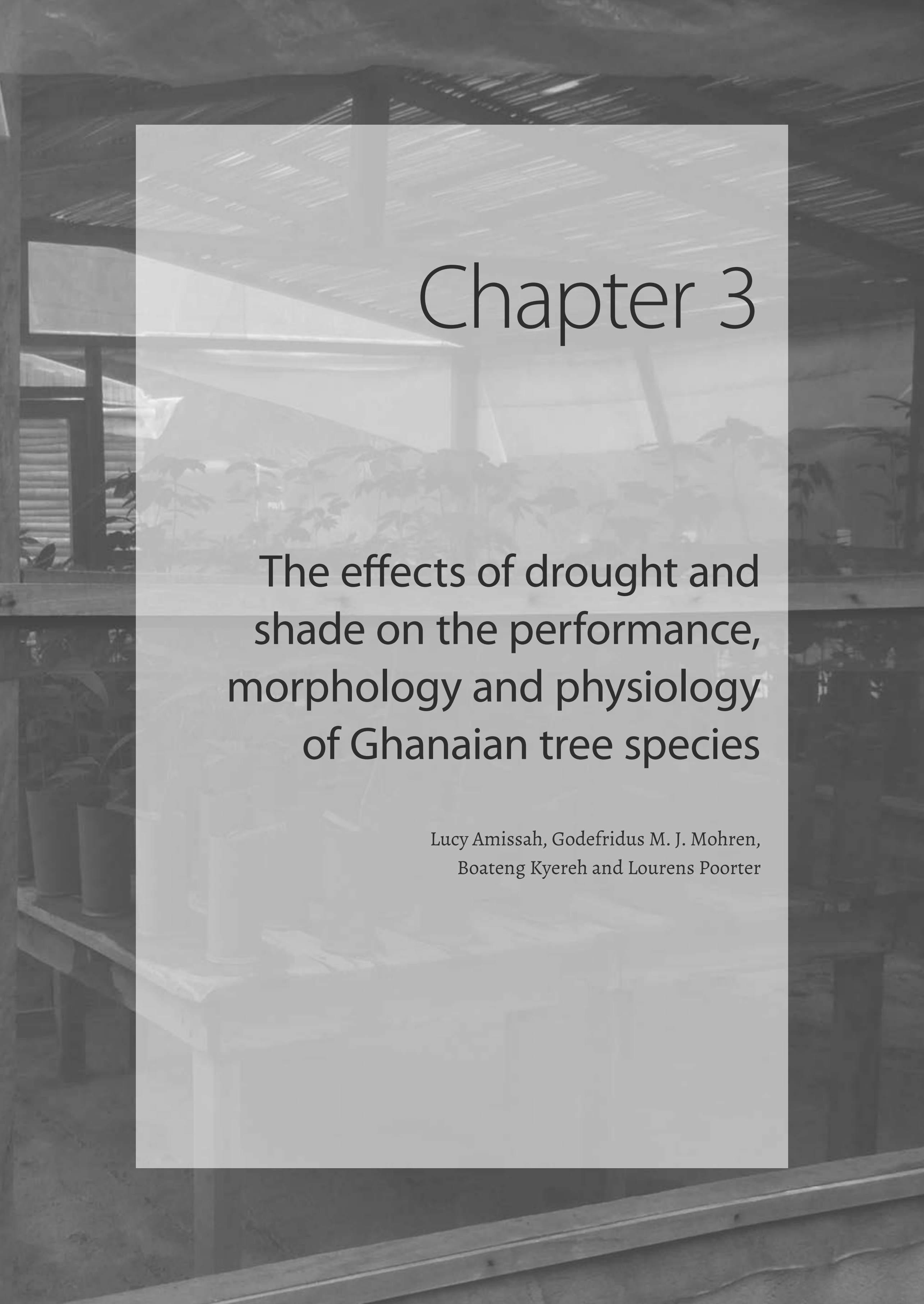
	RAN	RSEAS	TSEAS
RAN(mm)			
RSEAS(%)	-0.40***		
TSEAS (°C)	-0.60***	0.40***	
ISO (%)	0.80***	-0.60***	-0.60***

Appendix 4. Regression models fitted for presence absence data of 20 woody tree species of Ghana, the deviance (-2log likelihood), Nagelkerke R^2, significant levels, and model accuracy; Area Under the Curve (AUC). RAN = annual rainfall, RSEAS = rainfall seasonality, ISO = Isothermally, TSEAS = Temperature seasonality. Significant levels are at $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$., ns = not significant.

	Coefficient of variables											
	Constant	RAN	RAN^2	RSEAS	RSEAS^2	ISO	ISO^2	TSEAS	TSEAS^2	Deviance	R^2	AUC
Heritiera utilis	-1750***	0.17***	0.00005***	0.29***	-	44.3***	-0.31***	-	-	1360	0.42	0.89
Cynometra ananta	-490***	0.40***	0.00012***	2.91***	-0.02***	-	-	0.12***	0.00006***	880	0.47	0.92
Diospyros sanza-minika	-320***	0.25***	0.00008***	-0.76***	0.01***	0.33***	-	0.21***	0.00011***	1750	0.49	0.88
Pentadesma butyracea	-490***	0.33***	0.00010***	2.04***	-0.02***	-	-	0.30***	0.00016***	890	0.60	0.95
Entandrophragma angolense	43***	0.06***	0.00002***	-	0.00***	-	-	-	-	3110	0.18	0.73
Turraeanthus africanus	-50***	0.08***	0.00002***	-0.84***	0.01***	-	-	0.01***	-	2430	0.27	0.78
Petersianthus macrocarpus	-630***	-	-	-1.52***	0.01***	18.6***	-0.13***	-	-	2680	0.36	0.76
Ricinodendron heudelotii	14^{ns}	0.02***	0.00001***	-0.07	-	-	-0.00**	-0.03*	0.00001*	3250	0.11	0.65
Newbouldia laevis	140*	0.09***	0.00003***	-	-0.0***	-5.11*	0.03*	-	0.00***	1830	0.18	0.76
Mansonia altissima	1.2^{ns}	0.10***	0.00004***	-	-	-	-0.002***	-0.12***	0.00006***	1880	0.46	0.87
Nesogordonia papaverifera	-5.0^{ns}	0.02**	0.00001***	-	-0.00***	-	-	-	-	2680	0.28	0.78
Ceiba pentandra	220***	-0.00***	-	-0.07***	-	-5.72***	0.04***	-	-	3080	0.19	0.70
Celtis adolfi-friderici	-460***	-	0.000***	-	-0.00***	13.2***	-0.09***	-	-	2810	0.26	0.78
Albizia zigyia	4.3***	-	0.000***	-0.08***	-	-	-	-	-	2750	0.03	0.60
Pericopsis elata	-1080***	-0.02***	-	-	-	31.8***	-0.23***	-	-	333	0.40	0.95
Piptadeniastrum africanum	-57***	0.03***	0.00001***	-0.04*	-	0.23***	-	0.04*	0.00002***	2290	0.27	0.77
Antiaris toxicaria	14***	-	0.000***	-	-0.00***	-0.13***	-	-	-	3200	0.13	0.68
Strombosia pustulata	-370***	0.00***	-	-		9.90***	-0.07***	0.00**	-	2020	0.24	0.74
Terminalia ivorensis	-5.40^{ns}	0.03**	0.00001**	-0.89**	0.00**	0.12*	-	-	-	1490	0.06	0.65
Terminalia superba	-19***	0.03***	0.00001	-	-	-	-	-	-	3200	0.14	0.68

Appendix 5. Model and observed probabilities for three example species.

Variable	Model	Observed	Model	Observed	Model	Observed
Rainfall (mm y^{-1})	E. angolense	E. angolense	C. pentandra	C. pentandra	S. pustulata	S. pustulata
1197.81	0.26	0.13	0.68	0.92	0.76	0.27
1231.34	0.34	0.27	0.65	0.67	0.78	0.66
1284.00	0.46	0.45	0.61	0.66	0.80	0.63
1342.24	0.57	0.60	0.56	0.54	0.83	0.79
1404.83	0.64	0.71	0.50	0.55	0.85	0.82
1439.59	0.66	0.55	0.47	0.45	0.86	0.87
1465.78	0.67	0.73	0.45	0.44	0.87	0.90
1501.31	0.67	0.72	0.42	0.49	0.88	0.83
1543.85	0.66	0.73	0.38	0.49	0.89	0.89
1573.31	0.64	0.73	0.36	0.43	0.90	0.93
1597.75	0.62	0.61	0.34	0.39	0.91	0.89
1621.25	0.60	0.67	0.32	0.51	0.91	0.79
1638.77	0.57	0.58	0.30	0.37	0.92	0.90
1661.52	0.54	0.47	0.29	0.31	0.92	0.89
1707.42	0.45	0.39	0.26	0.25	0.93	0.93
1778.16	0.28	0.17	0.21	0.09	0.94	0.95
1856.21	0.12	0.31	0.17	0.18	0.95	0.91



Chapter 3

The effects of drought and shade on the performance, morphology and physiology of Ghanaian tree species

Lucy Amissah, Godefridus M. J. Mohren,
Boateng Kyereh and Lourens Poorter

Abstract

In tropical forests light and water availability are the most limiting factors for seedling growth and survival but an increasing frequency of drought may affect tree regeneration. Here, we present results of a greenhouse experiment, in which seedlings of 10 Ghanaian tree species were exposed to combinations of strong seasonal drought (continuous watering versus withholding water for nine weeks) and shade (5% irradiance versus 20% irradiance). We evaluated the effects of drought and shade on seedling survival and growth and plasticity of 11 underlying traits related to biomass allocation, morphology and physiology. Seedling survival under dry conditions was higher in shade than in high light, thus providing support for the *"facilitation hypothesis"* that shade enhances plant performance through improved microclimatic conditions, and rejecting the *trade-off hypothesis* that drought should have stronger impact in shade because of reduced root investment. Shaded plants had low biomass fraction in roots, in line with the *trade-off hypothesis*, but they compensated for this with a higher specific root length (i.e., root length per unit root mass), resulting in a similar root length per plant mass and hence similar water uptake capacity as high-light plants. The majority (60%) of traits studied responded independently to drought and shade, indicating that shade- and drought tolerance are not in trade-off, but largely uncoupled. This should provide ample opportunity for niche differentiation and species coexistence under a range of water and light conditions. Overall our results suggest that shaded tropical forest species may be able to survive under predicted increasing drought incidence.

Key Words: Relative growth rate, tropical forest, tree seedling, survival, phenotypic traits plasticity, leaf water potential.

INTRODUCTION

Seedling establishment, growth and survival play an important role in forest dynamics, as they determine the future composition of the forest canopy (Schiøtz *et al.* 2006). Seedling growth and survival are influenced by resource availability (i.e. light, water and nutrients), disturbance (fire, logging) and pests (herbivores and pathogens) (Marod *et al.* 2002, Duclos *et al.* 2013). In tropical forests light (Valladares *et al.* 2003) and water availability (Nepstad et *al.* 2004, Comita & Engelbrecht 2009) are spatially and temporally heterogeneous and this heterogeneity provides a productivity gradient (Sánchez-Gómez *et al.* 2006). At the upper end of the productivity gradient light is the most limiting resource, whereas at the lower end of the productivity gradient water is the most limiting resource (Sánchez-Gómez *et al.* 2006). For instance, in moist forests due to high moisture availability there is high productivity which leads to the formation of dense vegetation and results in a reduction in the amount of light that reaches the forest understorey. On the contrary, in drier forests where water is the most limiting resource there is low productivity which leads to the formation of a less dense forest canopy with more light reaching the forest understorey.

Seedling tolerance to limiting resources determines in part the forest composition and distribution of species. Over the past decades tropical forests have experienced a reduction in annual rainfall and in some areas, such as the Amazon forests, severe droughts have occurred (Malhi and Wright 2004, Saatchi *et al.* 2013). Climate change scenarios predict that the intensity and frequency of drought will even increase further in the near future (Cox *et al.* 2008, Sheffield and Wood 2008, Malhi *et al.* 2009, Lewis *et al.* 2011) and drought will be the main aspect of global change which will determine the future of moist tropical forests (Nepstad *et al.* 2004). Understanding species response to drought is therefore critical in forecasting possible impacts of climate change on regeneration in the forest and species distribution. In lowland tropical forest, species drought performance, tolerance and the length of dry season have been found to be important determinants of species distribution (Engelbrecht *et al.* 2007a, Baltzer *et al.* 2008, Sterck *et al.* 2014, Amissah *et al.* in press). The drought performance of a seedling may be influenced by the location (understory or gaps) where the seedling grows in the forest (i.e., its shade tolerance) (Veenendaal *et al.* 1996a). The drought interaction with shade may play an important role in how species establish, grow and survive, but information on the combined effects of drought and shade in the tropics is surprisingly scarce (but see Fisher *et al.* 1991, Burslem 1996, Veenendaal *et al.* 1996a).

Three contrasting views have been proposed on whether there is a trade-off between shade tolerance and drought tolerance. The *trade-off hypothesis* predicts a trade-off between shade and drought tolerance, because shaded plants invest in leaves to enhance light capture, but this comes at the expense of allocation to water acquiring roots, thus making shaded plants more sensitive to drought (Smith & Huston 1989). According to the *facilitation hypothesis* drought has a weaker impact on plants in shade, because of lower air temperatures and vapour pressure deficits in shaded microsites (Holmgren *et al.* 1997, 2000). Alternatively shade and drought tolerance are uncoupled and vary independently (the *uncoupled hypothesis*) across forest and shrub species (Holmgren 2000, Sack and Grubb 2002, Sack 2004, Sánchez-Gómez *et al.* 2006, Markesteijn & Poorter 2009). All plants require similar resources of light, water and nutrients for their survival, growth and reproduction (Poorter 2005). Consequently reduced availability in any one of the needed resources may lead to reduced survival and growth (*resource limitation hypothesis*). According to Brouwer (1963) plants will maximise their surface area to capture the most limiting resource (*Brouwer's hypothesis*). Differential capacity of plants species to maximise resource capture will be of significant ecological advantage in the face of changing global climate.

Functional traits may confer tolerance to shade and drought in several distinct ways (Sack *et al.* 2003). There are three main mechanisms for dealing with drought stress: (1) drought avoidance (2) drought delay and (3) physiological drought tolerance (Tyree *et al.* 2003, Poorter & Markesteijn 2008, Kursar *et al.* 2009, Markesteijn & Poorter 2009). Traits that are associated with drought avoidance include leaf shedding in deciduous species to reduce water loss. Evergreen species may also delay drought by increased below ground biomass allocation, construction of fine roots, and deep roots to enhance access to water (Poorter & Markesteijn 2008, Markesteijn & Poorter 2009). Evergreen plants could also produce thick leaves and reduce stomatal conductance to minimise transpirational water loss (Slot & Poorter 2007). Physiological drought tolerance is defined by a plant's ability to continue to function physiologically at low water availability (tolerance to low tissue water status). At low water potentials, drought tolerant species reduce the risk of xylem cavitation (through having dense stem with narrow vessels and pit pores), which allows them to maintain gas exchange and hydraulic conductivity (Engelbrecht & Kusar 2003, Tyree *et al.* 2003, Markesteijn & Poorter 2009).

Shade-grown plants typically invest in high above ground biomass (leaves and stem) and also make thin leaves to optimise light capture and utilisation (Reich *et al.* 1998, Evans & Poorter 2001, Gommers *et al.* 2013). At the whole-plant level shade-tolerant species also display their leaves efficiently to enhance light capture in a low light environment (Reich *et al.* 1998). Plants grown in high light allocate relatively less to leaves and allocate more to roots to capture water and nutrients to sustain the high transpiration rates and growth rates (Sims & Pearcy 1994, Poorter & Nagel 2000). These intraspecific responses of plants to shade are also mostly found in inter specific responses to shade among species. In spite of distinct strategies under shade and drought it is possible to have traits that confer both drought and shade tolerance in plants within a conservation resource strategy (Sánchez-Gómez *et al.* 2008, Sterck *et al.* 2011). In such a situation plants will have low allocation to leaves, high allocation to stem and produce thick roots for storage.

Phenotypic plasticity is the capacity of a genotype to alter its phenotype under changing environmental conditions (Valladares *et al.* 2007). Such plasticity may be of paramount importance for species to adjust to temporal and spatial variation in resource availability, but few studies have demonstrated to what extent plasticity is really associated with tolerance to shade and drought. In a study with eight Mediterranean woody tree species, Sánchez-Gómez *et al.* (2008) found that phenotypic plasticity was negatively related to shade tolerance (quantified as survival in deep shade), and not related to drought tolerance (quantified as survival under drought). In another study of 16 tropical rain forest shrub species in three light environments, Valladares *et al.* (2000) found that species, which specialise for gaps had higher plasticity than understory species. In gaps there is a predictable decrease in irradiance and plants respond plastically to these changes (Valladares *et al.* 2000a). Plasticity may be either adaptive or non-adaptive. If plasticity is adaptive, then a high plasticity would lead to higher survival under stressful conditions (Chapin *et al.* 1993).

In this study we evaluated in a controlled cross-factorial experiment the effects of light and drought on the performance, morphology and physiology of 10 Ghanaian tree species. We addressed three research questions: (1) what are the effects of drought and shade on seedling survival and growth? (2) What are the effects of drought and shade on underlying seedling traits, such as biomass allocation, morphology and physiology? (3) How does morphological plasticity relate to survival under stressful conditions and growth under optimal conditions? We hypothesised that (1a) with decreased resource availability (light, water) there will be decreased survival and growth (the *resource limitation hypothesis*, Quero *et al.* 2008], (1b) shade will result in increased drought survival compared to high light (the *facilitation hypothesis*, Holmgren (2000), (2) plants will invest in the organ that captures the most limiting resource (*Brouwer's hypothesis*, Brouwer 1963), (3) higher plasticity in plant functional traits should lead to high survival under stressful conditions (Chapin *et al.* 1993) and faster growth under optimal condition should lead to higher plasticity because plants have more carbon at their disposal to make plastic adjustment (Valladares *et al.* 2000, 2007).

MATERIALS AND METHODS

Species and study site

This study is part of a larger experiment in which we evaluated drought survival of 24 tropical tree species, and related it to their functional traits (Amissah *et al.* submitted). For the present study we focused on a subset of ten tropical forest species for which we were able to evaluate their acclimatisation responses to shade and drought. The 10 species come from 8 families with different distributions (moist, wet and dry forests) in Ghana's forests (Table 1). The species had different light requirements for regeneration: one pioneer, two shade tolerant and seven non-pioneer light demanders (Hawthorne 1995). The species were selected because of their importance for timber trade in Ghana, their use as medicinal plants, and because of their different rainfall distributions. Seeds of the species were collected from two forest types: moist forest (Bobiri Forest Reserve) and dry forest (Afram Headwaters Forest Reserve). The responses of the selected species to drought and shade were evaluated in 4 neutral shade greenhouses located at the Forestry Research Institute of Ghana (FORIG). The size of each greenhouse was 5.60 m x 4.96 m wide and 3 m high and inter-greenhouse distance was 4 m. A distance of 4 m was chosen so that neighbouring greenhouses would not shade each other. The green houses were aligned north-south to ensure that they all received the same amount of light at any point in time. Each greenhouse was covered with a plastic shelter, to avoid the entry of rain in the greenhouse.

Irradiance levels of 5% (2 greenhouses) and 20% (2 greenhouses) of full sunlight were created by using bamboo slats, mosquito netting and raffia mats. The irradiance levels were determined through daily measurements with a light meter (Fisher Scientific Traceable Dual Display light meter, Fisher Scientific, Pittsburgh, USA) for a month. Concurrent measurements of irradiance levels inside and outside of the greenhouses were made in the morning (8:00-9:00am), around noon (12:00-1:00pm) and in the afternoon (4:00-5:00pm). Irradiance level in each greenhouse was calculated as a percentage of irradiance outside the greenhouse. Daily average irradiance levels were calculated for each greenhouse. A monthly average was also calculated and was used as the irradiance level in each greenhouse. Twenty percent irradiance (20%) was used as this is typical for large forest gaps. Additionally, Agyeman *et al.* (1999) found that seedlings of Ghanaian tree species are able to achieve maximum growth at irradiances of between 10% and 44%; hence, 20% allows the comparison of species under "optimal" growth conditions. As a minimum irradiance we used 5% (which is typical for a small gap) instead of 1%-2% of full irradiance that is typical for the forest understory, because many non-pioneer light demanding species were included in the study, and these would not have survived the understory light levels.

In another greenhouse (of about 15% irradiance) seeds were germinated in germination trays filled with sandy loamy soils. The soil was collected from a moist forest (Bobiri Forest Reserve). The soils were not acidic and had an average pH of 6.5 (±0.28). The soils had moderate to high values of nitrogen, phosphorous, potassium and base saturation (see details of the chemical and physical properties of the soil in Appendix 1). Germinated seeds were then grown in 9 cm wide by 20 cm long PVC (Polyvinyl chloride) tubes filled with sandy loamy soils (1130 cm^3) collected from the moist forest. Sandy loam soil was preferred because it allows for good drainage, which is needed when plants are watered regularly. Seedlings were grown for three to four months before being transferred to the greenhouses. In the greenhouse, seedlings were allowed to acclimate for four weeks before they were subjected to watering and no-watering treatments. We recorded daily temperature and relative humidity (Appendix 2) over the period of the experiment using a Fisher memory hygrometer (Fisher Scientific, Pittsburgh, USA).

Table 1. List of ten tree species, their family, natural distribution and light requirements for regeneration (species guild). NPLD = non-pioneer light demander. Species guild and preference for a different forest type is based on Hall & Swaine (1981), Hawthorne (1995), Hawthorne & Jongkind (2006) and Hawthorne & Ntim Gyakari (2006).

Species	Family	Forest type	Species guild
Entandrophragma angolense (Welw). DC	Miliaceae	Moist forest	NPLD
Turraeanthus africanus (Welw. ex C.DC.) Peller	Miliaceae	Moist forest	Shade tolerant
Piptadeniastrum africanum (Hook.f.) Brenan	Mimosaceae	Moist forest	NPLD
Ceiba pentandra (Linn.) Gaertn.	Bombaceae	Dry forest	Pioneer
Albizia zygia (DC.) J.F. Macbr.	Mimosaceae	Dry forest	NPLD
Pericopsis elata (Harms) Van Meeuwen	Pailionaceae	Dry forest	NPLD
Sterculia rhinopetala K. Schum	Sterculiaceae	Dry Forest	NPLD
Aningeria robusta (*Pouteria aningeri*) *(A. Chev.)Aubrev. and Pellegr.*	Sapotaceae	Dry Forest	NPLD
Antiaris toxicaria Leschenault	Moraceae	Ubiquitous	NPLD
Strombosia pustulata J. Leonard	Olacaceae	Ubiquitous	Shade tolerant

Experimental design.

The design in the greenhouse was completely randomised factorial design with water, light and species as factors. We studied 96-112 individuals per species, which were randomly assigned to- and equally distributed amongst the four greenhouses; half of the individuals of each species in each greenhouse received water, and the other half were not watered for nine weeks. We simulated therefore not continuous low water conditions, but the effect of a prolonged dry season drought. Rainfall records taken from a rain gauge placed at 3 km from a dry semi-deciduous and a wet evergreen forests in the study region over a period of two years indicated a two-month period (December to January) in which there was no rain, especially in the dry forest (L. Amissah, unpublished data). Therefore the nine weeks that water was withheld from seedlings in the greenhouse compares with dry season in the field. The experiment included in total 1,056 seedlings (6 species x 2 light treatments x 2 greenhouses x 2 drought treatments x 14 seedlings per treatment combination + (4 species x 2 light treatments x 2 greenhouses x 2 drought treatments x 12 seedlings per treatment combination). The positions of individual seedlings were rotated in the greenhouse every two weeks to ensure all species were exposed to the same environmental variation in the shade house. Because of limited seed availability and space constraints the experiment was conducted in two batches; the first was conducted from August-November 2010 and the second from February–

May 2011. One additional species (*Ricinodendron heudelotii)* was included as a phytometer in both batches of the experiment to test for any systematic differences in the growing conditions in the greenhouses. A Mann Whitney U test of the differences in percent survival (in the dry treatment) between *Ricinodendron heudelotii* seedlings in the first and second batches of the experiment for low and high light treatments at the end of nine weeks did not show significant difference (Low light, Mann Whitney $U = 39.50$, $Z = -0.11$, $P = 0.92$, $n = 19$; high light, $U = 40.0$, $Z = -0.05$, $P = 1.00$, $n = 19$).

Seedling performance and traits measurements

At the beginning and end of the experiment, randomly, eight individuals were selected for each species and their heights, diameters, leaf areas, stem and root lengths were measured and leaves counted. Leaves were digitised with a desktop scanner (Canon Lide 100) and leaf area was determined with pixel counting software Image J (Schneider *et al.* 2012). Total root length was measured using the line intersect method (Newman, 1966). Fresh weights of leaves, stems and roots were determined and the samples dried in an oven at 65°C for 48 hours. Relative growth rate was calculated for each species using initial and final harvest at the end of nine weeks using equation 1 (Hoffman and Poorter 2002).

$$\text{RGR plant dry mass} = (\overline{\text{lnPD2}} - (\overline{\text{lnPD1}}))/(t2 - t1) \qquad \text{Equation 1}$$

where $\overline{\text{lnPD1}}$ and $\overline{\text{lnPD2}}$ are the means of natural logarithm transformed plant dry mass at time t_1 and t_2.

The basic measurements were used to calculate nine seedling traits: leaf mass fraction (LMF; total leaf mass divided by plant mass, g g^{-1}), stem mass fraction (SMF, stem mass divided by plant mass, g g^{-1}), root mass fraction (RMF, root mass divided by plant mass, g g^{-1}), specific leaf area (SLA, leaf area per leaf mass, cm^2 g^{-1}), leaf area ratio (LAR, total leaf area divided by plant mass, cm^2 g^{-1}), specific stem length (SSL, stem length divided by stem mass, cm g^{-1}), specific root length (SRL, total root length divided by root mass, cm g^{-1}), stem length per unit plant mass (SLPM, stem length divided by plant mass, cm g^{-1}) and root length per unit plant mass (RLPM, total root length divided by plant mass, cm g^{-1}). Leaf traits (LMF, SLA, and LAR), were calculated because of their importance for light capture, and stem traits (SSL and SLPM) because of their importance for vertical height expansion and hence, light capture (Poorter 1999), and for water transport and stability. The root traits (RMF, SRL and RLPM) were chosen because they are important for water capture (Poorter & Markesteijn 2008), and for water storage (RMF).

Assessment of survival, wilting and physiological measurements.

Seedling survival was assessed every week. Seedling wilting stage was monitored following Tyree *et al.* (2002). Mid-day leaf water potential (ψ_{mid}) was measured for six slightly wilted individuals of each species in each greenhouse using the pressure bomb technique (Tyree & Hammel, 1972). Stomatal conductance was measured on the same selected individuals using leaf porometer (Model SC-1, Decagon Devices, USA). Similar measurements of stomatal conductance and leaf water potential were performed for the watered plants. Leaf water potential was measured because it gives an indication of the level of water stress in a plant and stomatal conductivity was chosen because it gives an indication to what extent plants are photosynthetically active at that stress level, and how plants control water loss through stomatal closure. Drought survival in shade and in high light was quantified as the percentage of individuals alive in the dry low light- and dry high light treatments at the end of the experiment.

Data analysis.

A Mann-Whitney (exact test) was used to test the differences between drought survival in the shade (5% irradiance) and under dry treatment and drought survival in high light (20% irradiance) and under dry treatment after nine weeks. A three-way ANOVA was performed to evaluate the effects of species, light and water on relative growth rate and leaf physiology. Species, light and water were used as factors and RGR, leaf water potential and stomatal conductance as dependent variables. Greenhouses were not included as a factor in the final three-way ANOVA because the difference in the light treatment was large (5%-20%) and species values differed little between the two greenhouses belonging to the same light treatment. Data from each replicates of light level was pooled together. An ANCOVA was performed to evaluate the effects of light and water on morphological traits. Plant dry mass was included as a covariate to correct for ontogenetic effects due to variation in seedling size (cf. Poorter 1999). Allocation variables (LMF, SMF, and RMF) are proportional (between 0 and 1) and they were therefore arcsine transformed to enhance normality and to stabilise the variance. The other traits (SLA, SSL, SRL, LAR. SLPM, RLPM, stomatal conductance and leaf water potential) were $\log_{10}$ transformed to stabilise the variance. Plasticity was calculated by first taking the average trait value of each of the four treatment combinations (dry and low light, dry and high light, wet and low light, wet and high light). Plasticity was then calculated for each trait as the difference between maximum mean value and minimum mean value of the treatment combinations, divided by the maximum mean value (Valladares *et al*. 2000). The relationship between overall plasticity index (mean of trait plasticity of the 9 individual traits) and growth under optimum conditions (high light, 20% irradiance and daily watering) was tested using Spearman correlation. Additionally, the relationship between overall plasticity index and survival under stressed conditions (high light, 20% irradiance and drought for nine weeks) was tested using Spearman correlation. Plasticity of each of the 9 individual traits was also correlated with survival under stressed conditions and growth under optimal conditions, using species as data points.

RESULTS

Seedling survival and relative growth rate in response to drought and shade.

Drought led to a decrease in survival compared to the continuously watered plant in both shade (89% drought survival versus 100% for continuously watered plants) and light (53% drought survival versus 99.8% for continuously watered plants). No statistical test was carried out to test the difference in survival in the watered plants because survival was 100% in the 5% irradiance greenhouse and 99.8% in the 20% irradiance greenhouse. There was significant difference between drought survival in the shade (5% irradiance) and drought survival in the high light (20% irradiance) in the dry treatment (Mann-Whitney $U = 10.5$, $Z = -2.99$, $P < 0.01$). Drought survival in high light was 1.7 fold lower than in shade, indicating that plants are hit harder by drought in exposed environments that are typical of gaps (Fig.1a). Both drought and shade led to a decrease in relative biomass growth rate (Three-way ANOVA, drought, $P \leq 0.001$; shade $P \leq 0.001$; Fig.1b). There was a significant interaction effect ($P \leq 0.001$) of light and water on relative growth rate, indicating that the effect of drought depended on the light level under which plants were growing. Drought reduced relative growth rate more strongly under high light than in low light.

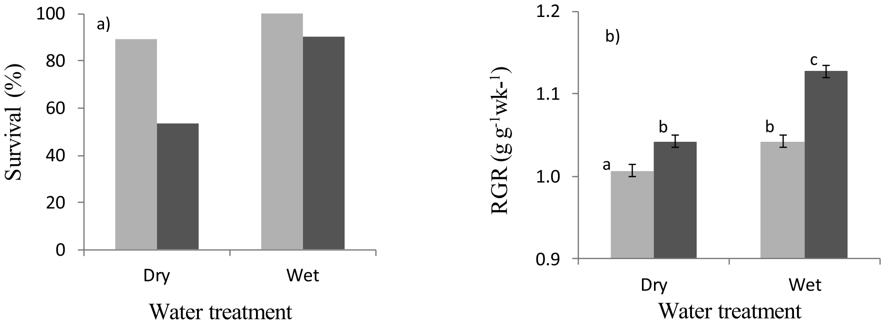


Figure 1. Performance of Ghanaian tree seedlings in terms of (a) survival and (b) relative biomass growth rate (RGR) in response to drought and shade. Shade treatments consisted of low light (5% of full sunlight, grey bars) and high light (20% of full sunlight, black bars). The water treatment consisted of a wet treatment (plants continuously watered for nine weeks) and dry treatment (water was withheld from seedlings for nine weeks). Means and standard error of the means are shown. Bars accompanied by a different letter are significantly different at $P < 0.05$ (ANOVA, Post hoc LSD test). n = 10 species.

Drought and shade effects on allocation and morphology

Seedling responses were analysed with a three-way ANCOVA, with species, light, and water as factors, and plant dry mass at harvest as a covariate (Table 2). Overall the models explained a substantial part of the variation (average R^2: 0.78, R^2 range: 0.61- 0.93). Biomass at final harvest did not have an effect on biomass allocation, but it had a strong effect on tissue morphology and whole-plant morphology (Table 2). Overall, species had the strongest effect on seedlings, affecting all traits, with high F values. Of the environmental factors, light had the strongest effect on seedlings, affecting 92% (11/12) of the traits evaluated. Water had a significant effect on 70% (7/10) of the traits evaluated, whereas there were considerably less significant interactions between light and water (40% of the cases, 4/10), and for those the *F* values were also much lower.

Drought effects on allocation and morphology

Drought did not alter leaf mass fraction ($P = 0.115$; Fig. 2a) which indicates that the transpiring leaf mass is not reduced under drought. The effects of drought on specific leaf area, and leaf area ratio could not be determined because leaves of seedlings were wilted at final harvest. There was no significant effect of drought on stem mass fraction ($P = 0.066$; Fig. 2d) but drought led to an increase in specific stem length ($P \leq 0.001$; Fig. 2e) and stem length per unit plant mass ($P \leq 0.001$; Fig. 2f). Drought led to high allocation to roots (Root mass fraction, $P = 0.018$; Fig. 2g), no significant change in specific root length ($P = 0.423$; Fig. 2h) and a significantly higher root length per unit plant mass (P = 0.005; Fig. 2i) which facilitates water uptake.

Shade effects on allocation and morphology

Shade led to an increase in allocation to leaves (high leaf mass fraction, $P \leq 0.00$; Fig. 2a), increased production of thin and/or soft leaves (high specific leaf area, $P \leq 0.001$; Fig. 2b) and increased the leafiness of the seedlings (high leaf area ratio, $P \leq 0.001$; Fig. 2c) thus enhancing light capture. Shade led to a reduction in allocation to stem (low stem mass fraction, $P = 0.025$; Fig 2d), an increase in specific stem length ($P \leq 0.001$; Fig. 2e) and stem length per unit plant mass ($P \leq 0.001$; Fig 2f). Shade decreased allocation to roots (low root mass fraction, $P \leq 0.001$; Fig. 2g) and increased investment in fine roots (high specific root length, $P \leq 0.001$; Fig 2h). Hence, the lower investment in root biomass was compensated for by investment in a higher specific root length which resulted in a similar root length per plant mass for shaded plants compared to light plants ($P = 0.817$; Fig. 2i).

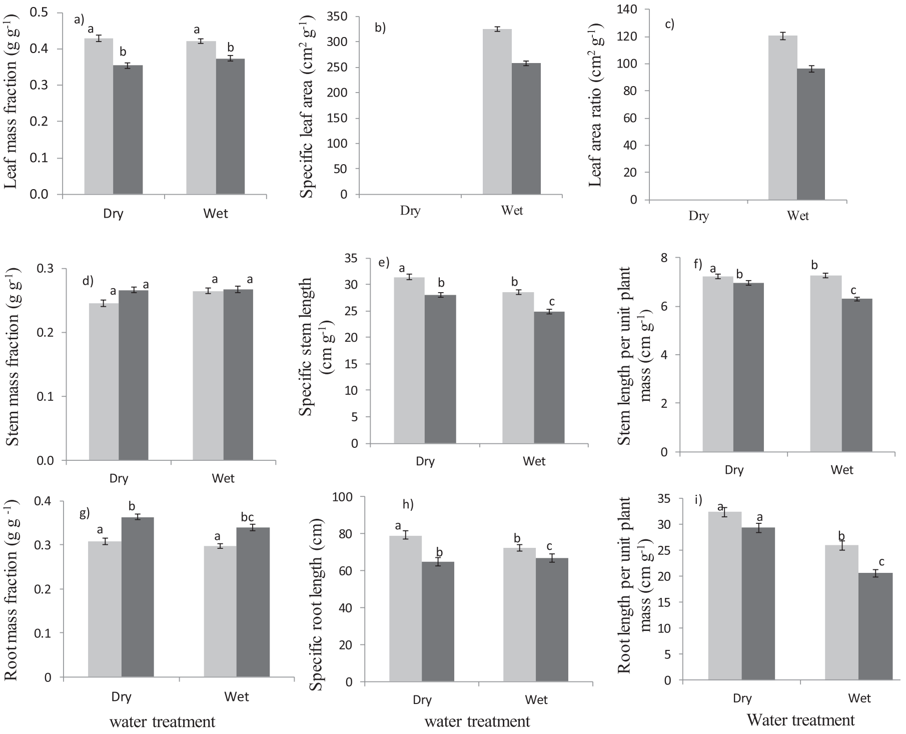


Figure 2. Seedling responses to drought and shade in terms of allocation (left panels), tissue morphology (middle panels) and whole-plant efficiency (right panels) for leaf- (top panels), stem- (middle panels) and root (lower panels) tissues. Shade consisted of low light (5% of full sunlight, grey bars) and high light (20% of full sunlight, black bars). The drought treatment consisted of a wet treatment (plants continuously watered) and dry treatment (water was withheld from plants for nine weeks). (a) leaf mass fraction (LMF), (b) specific leaf area (SLA), (c) leaf area ratio (LAR), (d) stem mass fraction (SMF), (e) specific stem length (SSL), f) stem length per unit plant mass (SLPM), (g) root mass fraction (RMF), (h) specific root length (SRL), and (i) root length per unit plant mass (RLPM). Means and standard errors are shown. Bars accompanied by a different letter are significantly different (ANCOVA, Turkey's test $P<0.05$). n = 10 species. For droughted plants no bars are shown for SLA and LAR, because the leaves were desiccated, and their leaf area could not be measured precisely.

Table 2. A Three- way ANOVA of species (S, df = 9), water (W, df = 1) and light (L, df = 1) as main factors and relative growth rate, biomass allocation, morphological and leaf physiological traits as dependent variables. Plant dry mass was included in the ANOVA as a covariate for all variables but RGR, and beta is the regression coefficient of the slope. F-value, significance levels and R^2 of the model are shown. *: $p \leq 0.05$, **: $p \leq 0.01$, ***: $p \leq 0.001$, ND = not determined. Leaf mass fraction, stem mass fraction and root mass fraction were arcsine transformed and all other traits were $\log_{10}$ transformed prior to analysis.

Traits	beta	Plant dry mass	Species	Light	Water	SX L	SXW	LXW	SX L XW	R^2
Relative growth rate		ND	20.6^{***}	81.9^{***}	85.6^{***}	0.9	6.3^{***}	13.4^{***}	0.9^{***}	0.92
Leaf mass fraction	0.02	0.8	105.7^{***}	53.2^{***}	2.5	7.1^{***}	11.6	4.2^{*}	4.0^{***}	0.69
Specific leaf area	-0.15	33.1^{***}	58.5	14.6^{***}	ND	3.9	ND	ND	ND	0.66
Leaf area ratio	-0.14	17.5^{***}	46.8^{***}	34.5^{***}	ND	3.9^{***}	ND	ND	ND	0.69
Stem mass fraction	-0.02	1.5	190.5^{***}	5.0^{*}	3.4	5.6^{***}	7.6^{***}	3.9^{*}	2.7^{***}	0.77
Specific stem length	-0.62	1079.5^{***}	67.9	50.9^{***}	35.6	5.9	3.8	0.6	1.6	0.91
Stem length per unit plant mass	-0.64	1741.4^{***}	275.5^{***}	38.9^{***}	10.7^{***}	3.8^{***}	5.0^{***}	18.3	1.4	0.93
Root mass fraction	-0.01	0.2	52.2^{***}	44.6^{***}	5.7^{*}	5.1^{***}	5.1^{***}	1.4	1.6	0.61
Specific root length	-0.33	79.2^{***}	86.4^{***}	16.6^{***}	0.6	1.3	6.4^{***}	3.9^{*}	2.4^{*}	0.69
Root length per unit plant mass	-.33	87.8^{***}	113.5^{***}	0.1	8.1^{*}	1.3	10.2^{***}	3.1	2.4^{*}	0.77
Stomatal conductance	ND	ND	26.3^{***}	72.9^{***}	873.1^{***}	6.4^{***}	12.9^{***}	1.9	3.4^{*}	0.91
Leaf water potential	ND	ND	33.3^{***}	10.4^{***}	182.7^{***}	4.8^{***}	5.4^{***}	0.0	3.1^{*}	0.79

Combined impact of shade and drought on allocation and morphology

Forty percent (40%) of the variables showed an interaction of light and water, as demonstrated by ANCOVA analysis (Table 2). Relative growth rate ($P \leq 0.001$), leaf mass fraction ($P \leq .05$), stem mass fraction ($P = 0.05$) and specific root length ($P = 0.048$) were traits that responded to the combined effects of light and water. This indicates that relatively few variables responded to the combined effects of shade and drought. Drought reduced relative growth rate more strongly in high light than in low light and for stem mass fraction drought resulted in a stronger reduction in shade than in high light. For specific root length drought led to an increase in SRL in low light but a decrease in high light. For leaf mass fraction drought led to a stronger reduction in high light than in shade.

Leaf physiology

Stomatal conductance and mid-day leaf water potential of slightly wilted seedlings showed significant response to drought and shade (Table 2). Drought led to a strong reduction ($P \leq 0.001$) in stomatal conductance of the leaves that were slightly wilted (Fig. 3a). Shade led to a reduction ($P \leq 0.001$) in stomatal conductance (Fig. 3a). Leaf water potential decreased in response to drought ($P \leq 0.001$) but did not change with shade ($P = 0.090$) and there was no significant light x water interaction ($P = 0.938$; Fig. 3b).

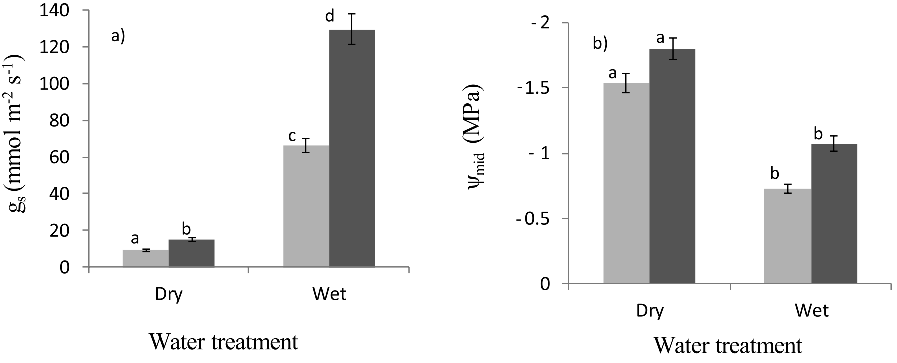


Figure 3. Seedling leaf physiological traits: (a) stomatal conductance (g_s), (b) midday leaf water potential (ψ_{mid}) of plants from which water was withheld and plants that received daily watering for 9 weeks in 5% of full sunlight (grey bars) and 20% of full sunlight (black bars). Bars are means and error bars are standard errors of the means.

The relationship between trait plasticity and species performance

To evaluate whether trait plasticity was associated with seedling performance it was correlated with RGR under optimal conditions (wet treatment in 20% light), survival under stressed condition (dry treatment in 20% light) and plasticity in RGR and survival. RGR under optimal conditions was only significantly correlated with plasticity in RMF ($r = 0.81$, $P \leq 0.01$; Table 3, Fig. 4 d). Survival under stressful conditions was only significantly and positively correlated with plasticity in leaf mass fraction (Fig. 4b, $r = 0.74$, $P = 0.014$). Plasticity in survival was significantly negatively related to plasticity in leaf mass fraction ($r = -0.71$, $P = 0.023$). Plasticity in RGR was not significantly related to plasticity of any of the traits (Table 3).

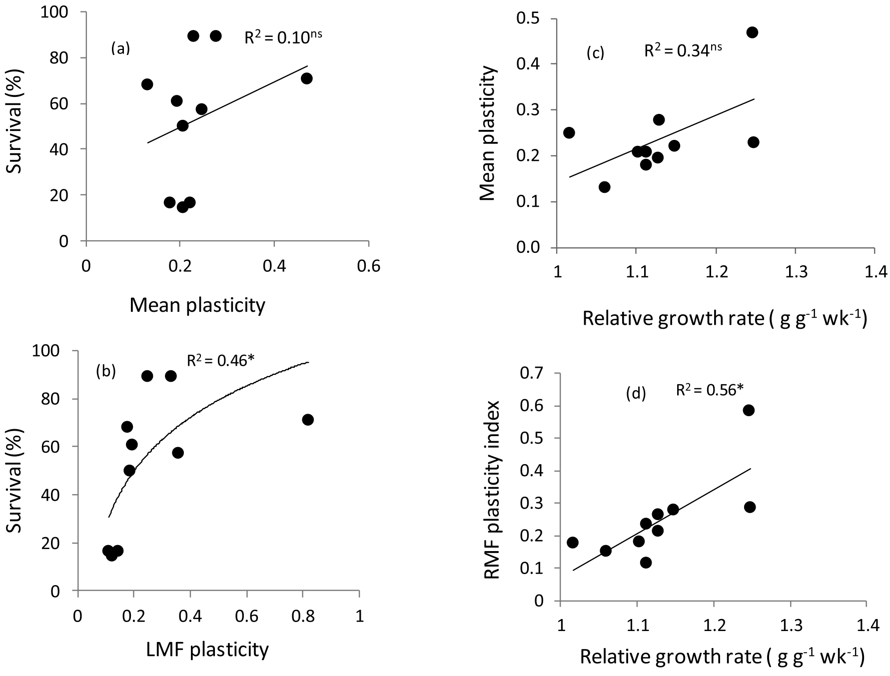


Figure 4. Relationship between survival under stressful conditions (drought and high light) and (a) mean plasticity of nine traits, (b) Leaf mass fraction (LMF) plasticity. Relationship between relative growth rate under optimal conditions (continuous watering and 20% of full sunlight) and (c) mean plasticity and (d) root mass fraction plasticity. Plasticity for each trait was calculated as maximum minus minimum mean trait values divided by maximum mean trait values across four treatment combinations. For each species, mean plasticity was calculated as the average plasticity of 9 traits. Regression line and coefficient of determination are shown. Ns = not significant, * = p ≤ 0.05, ** = p ≤ 0.01, n = 10 species.

Table 3. Spearman rank correlation between plasticity in functional traits and seedling performance of 10 Ghanaian tree species; their relative growth rate under optimal conditions (20% of full sunlight and nine weeks watering), plasticity in relative growth rate, survival under stress conditions (no watering for 9 weeks in 20% of sunlight), plasticity in stress survival, and mean plasticity across four treatment combinations (5% of sunlight and no watering, 20% of sunlight and no watering, 5% of sunlight and watered, and 20% of sunlight and watered). n = 10 species. Significance levels of the correlation are shown. *: $p \leq 0.05$, ***: $P \leq 0.001$. RGR = Relative Growth Rate.

Plasticity trait	RGR (optimum)	Plasticity RGR	Stress survival (%)	Plasticity survival
Leaf mass fraction	0.19	0.13	0.74^{*}	-0.71^{*}
Stem mass fraction	-0.08	0.08	-0.45	0.61
Root mass fraction	0.81^{**}	0.54	0.32	-0.32
Specific leaf area	-0.07	-0.15	-0.52	0.46
Specific stem length	0.13	0.16	0.01	-0.20
Specific root length	0.59	-0.14	0.56	-0.43
Leaf area ratio	0.07	-0.16	0.02	-0.07
Stem length per unit plant mass	0.62	0.19	0.35	-0.37
Root length per unit plant mass	0.58	-0.02	0.53	-0.49
Overall mean plasticity	0.47	-0.03	0.43	-0.38

DISCUSSION

Here we discuss the effects of drought and shade on the performance, morphology and physiology of tree seedlings and the effects of carbon gain on plasticity in traits and how plasticity in traits relates to survival of species under stressed conditions.

Seedling performance in response to drought and shade.

We hypothesized that drought and shade would reduce seedling growth and survival because of a lower resource availability (the *resource limitation hypothesis*), and that drought survival would be higher under shade than in high light because of improved microclimatic conditions (the *facilitation hypothesis*). Our results support both hypotheses (Fig.1). The weaker impact of drought in shade is consistent with the facilitation hypothesis of Holmgren *et al.* (2000) and other studies in which drought sensitive seedlings growing under herbaceous layer in Californian Chaparral had high survival (Moreno & Oechel 1992, Sack 2004). Under shaded conditions plants are exposed to low air temperatures and low vapour pressure deficits resulting in less drought stress and enhanced drought survival (cf. Thomas & Davis 1989, Holmgren *et al.* 2000, Sack 2004). Our results contrast with the *trade-off hypothesis* of Smith & Huston (1989), who state that drought should have *stronger* impact in the shade than in high light, because shaded plants invest relatively less in roots, and have therefore less access to soil water. We indeed found that shaded plants had lower RMF, in line with Smith & Huston's hypothesis, but they compensated for this with a higher specific root length, resulting in a similar root length per plant mass, and hence capacity for water uptake, as high-light plants (Fig. 2 h, i).

Under field conditions an enhanced survival below shaded tree crowns can also result from an increased nutrient input by tree litter (Holmgren *et al.* 1997). In the understory of tropical forests, saplings growing under tree crowns invest in long-lived leaves which are characterized by high levels of defense against herbivores (Coley Barone 1996). Other studies found contrasting results; drought survival in the understory was lower compared to plants growing in the centre of a forest gap (Veenendaal *et al.* 1996a) in West Africa in line with the trade-off hypothesis. Such findings could partly be attributed to the fact that plants in shade suffer from competition for water uptake by canopy trees (Wright *et al.* 2003). The enhanced drought survival in shade that we found might allow these species to persist in the forest understory as the climate becomes drier in the future. We should emphasize that this is a greenhouse study where plants were grown in a limited soil volume, and under field conditions other drought-coping mechanisms might become important as well. For instance plants growing in high irradiance in the field will take advantage of their fast growth and large size at the end of the wet season. As a result, they can forage during the dry season a larger soil volume, or deeper soil layers for water, where it is more readily available (Poorter & Hayashida 2000, Sack 2004).

Both drought and shade reduced relative growth rate which is in agreement with our *resource limitation* hypothesis, and consistent with other studies of Mediterranean species growing in the field or under controlled conditions (Sack & Grubb 2002, Quero *et al.* 2008, Sack 2004). We found that shade reduced RGR more strongly in wet- compared to dry conditions, which contrast with the findings of Sack & Grubb (2002) and Sack (2004) who found proportional reduction of RGR in low light and high light (*i.e.* no interaction effect).

Morphological and physiological response of seedlings to drought

We hypothesized that plants will invest in the organ that captures the most limiting resource (*Brouwer's hypothesis*). Generally species growing in drier environment may improve water capture through investment of more biomass in roots and the production of thin roots with high specific root length (SRL) and an increase in root length per unit plant mass (RLPM) at the whole plant level (Poorter & Markesteijn 2008). We indeed found that under drought seedlings had higher RMF and RLPM, in line with *Brouwer's hypothesis*, although they did not produce roots with high SRL (Table 2; Figs. 2g,i). In a study of thirteen temperate species, reduction in watering led to an increase in RMF (Sack 2004) but in another study of four temperate shade-tolerant species no significant difference in LMF, SMF and RMF were found across watering treatments (Sack & Grubb 2002). Roots are, apart from water uptake, also important for water storage. For example, seedlings of Baobab provenances from drier areas had higher RMF (De Smedt 2012), which allowed them to store more water, and realize higher conductance and photosynthetic rates during drought.

In our study, drought led to increased drought stress as indicated by more negative mid-day leaf water potentials, and lower stomatal conductance (Fig. 3a). The lower stomatal conductance implies reduced assimilation rate, (cf. Wright *et al.* 1992, Cao 2000, Aranda *et al.* 2005) which also explain the reduced growth of droughted plants (Fig. 1). According to Allen *et al.* (2010) there is a continuum of stomatal responses to drought which ranges from drought avoidance, in which the stomata close at a threshold water potential to reduce transpiration and cavitation, to drought tolerance in which stomatal control is less severe and leads to higher transpiration rate (cf. McDowell *et al.* 2008).

Plant may also reduce water loss during drought by reducing biomass fraction in transpiring leaves. This strategy was not confirmed in our study, as there was no significant change in leaf mass fraction in response to drought. We could not evaluate the effects of drought on SLA and LAR (see methods) but other studies found that seedlings that grow under dry conditions have low SLA and LAR which help to reduce water loss through transpiration (Poorter & Markesteijn 2008). In another study, water stress did not have an effect on SLA (Aranda *et al*. 2005).

Morphological and physiological response of seedlings to shade

In low irradiance light is a limiting resource, and shaded seedlings had higher LMF, SLA and LAR and, hence, higher light capture, in line with *Brouwer's hypothesis* (cf. Givnish 1988; Walters & Reich 1999, Evans & Poorter 2001). Shaded plants invested less biomass in stems, which could curtail their ability to overtop neighbours and access light. Yet, they compensated for this by producing slender stems with high specific stem length, leading to a higher stem length per unit plant mass (Fig. 2e, f). Such an etoliation response to shading has also been found for other tree seedlings (Poorter 1999).

The increased biomass allocation to leaves in the shade came not only at the expense of a reduced biomass allocation to stem, but also at the expense of reduced biomass allocation to roots (Fig. 2g). This is seemingly in line with Smith & Huston's (1989) *trade-off hypothesis*, which states that an increase in shade tolerance comes at the expense of an increase in drought tolerance. Yet, shaded plants compensated for a reduced RMF by producing fine roots, leading to similar root length per unit plant mass, and hence, to a similar ability to capture water. The higher LAR and SLA of shaded plants could potentially lead to a higher evaporative load, but this is compensated for by the low air temperature and vapour pressure deficit in the shade (Sack & Grubb 2002).

Leaf water potential was more negative in high light compared to the shade (Fig. 3b), indicating that high-light plants are more water-stressed probably because of higher temperatures and vapour pressure deficits. At the same time the stomatal conductance was higher, indicating that stomata are also sensitive to the amount of light. The high stomatal conductance facilitates higher assimilation rates, and therefore faster growth rates in high-light compared to shaded plants (Fig. 1). The results of the study is consistent with findings of a study of Aranda *et al.* (2005) in which both watered and droughted seedlings showed higher stomatal conductance under high light conditions.

Combined effects of shade and drought on plant

Our study results showed within species performance trade-off between survival and growth as seedlings growing in the shade in drought had high survival but low relative growth rate compared to seedlings growing in high light, which is in agreement with the growth-survival trade-off found for seedlings and saplings across tropical tree species (Wright *et al.* 2003, Baraloto *et al.* 2005). A trade-off in biomass allocation was found in our study as plants in shade allocated more biomass to leaves and plant in drought allocated more biomass to roots. Similar trade-offs have been found for other studies across 806 temperate tree species (Niinemets & Valladares 2006) and across tropical species of Bolivia (Poorter & Markesteijn 2008) where seedlings of species from drier forest allocated more biomass to roots, whereas seedlings of species from moist forest allocated more biomass to leaves. Although our study focused on intraspecific responses compared to the other studies mentioned here, we make these comparisons because intraspecific acclimatisation found within species parallel adaptation responses found across species. For most of the traits we studied there was no significant interaction between shade and drought indicating that drought and shade tolerance can vary independently. Seedlings were able to tolerate combined shade and drought probably as a result of investment in organs that help to reduce demand for resources (Sack *et al.* 2003). Our leaf water potential data suggest that shade alleviates drought impacts (although we did not find a significant shade x drought interaction) which contrasts sharply with the results of Valladares & Pearcy (2002) who found a greater decline of leaf water potential with drought stress in the shade than in the sun. Perhaps this is because their study was carried out in an unusually dry El Niño year in Central California.

Relationship between plant trait plasticity and seedling performance

We hypothesized that higher plasticity in plant functional traits will lead to high survival under stressed conditions (Chapin *et al.*1993). This hypothesis was rejected, as overall plasticity index across our treatment combination was not significantly related to survival under stressful conditions (Fig. 4a). Sanchez-Gomez *et al.* (2008) neither found a relationship between overall phenotypic plasticity in response to water availability and enhanced performance under drought. Plasticity in traits is not always an adaptive feature of plants, but in situation where it is considered adaptive feature it should lead to higher survival under stressful condition (Chapin *et al.*1993). In our study, plasticity in leaf mass fraction was significantly related to survival under stressful conditions (Fig 4b). Perhaps the plasticity of individual key traits is more important in influencing species survival than a combination of traits. Adjusting the transpiring leaf mass may be an important mechanism to adjust to reduced water availability. Deciduousness, for example, has been found to be one of the determinants of drought survival (Poorter & Markesteijn 2008). A positive correlation between percent leaf loss and drought survival has also been found among individuals across three evergreen species in Australia (Deines *et al.* 2011).

We also predicted that faster growth under optimal condition would lead to higher plasticity (Valladares *et al.* 2000, 2007) because under high resource availability more carbon is produced and can be invested for traits adjustments in response to changing environment (cf. Valladares *et al.* 2000, 2007). Yet, fast growth was not related with a higher overall plasticity. It was related with a high RMF. The ability of plants to show plastic responses to environment may in part define the ecological niche width of species (Saldaña *et al.* 2005) and species with higher plasticity in water balance related traits will more likely acclimatise to global climate change.

CONCLUSIONS

Shaded plants survive drought better than plants in high light but they do so at the expense of their relative growth rates. Our results suggest that shaded tropical forest species may be able to survive under predicted reduction in rainfall. A greater percentage (60%) of traits studied responded independently to drought and shade which allows for niche differentiation under any combination of water availability and shade. Overall traits plasticity was not related to survival under stressed condition though plasticity in leaf mass fraction was significantly related to survival under stressful conditions. Plasticity of individual traits that are associated with water balance may play a role in how seedlings survive under drought and shade.

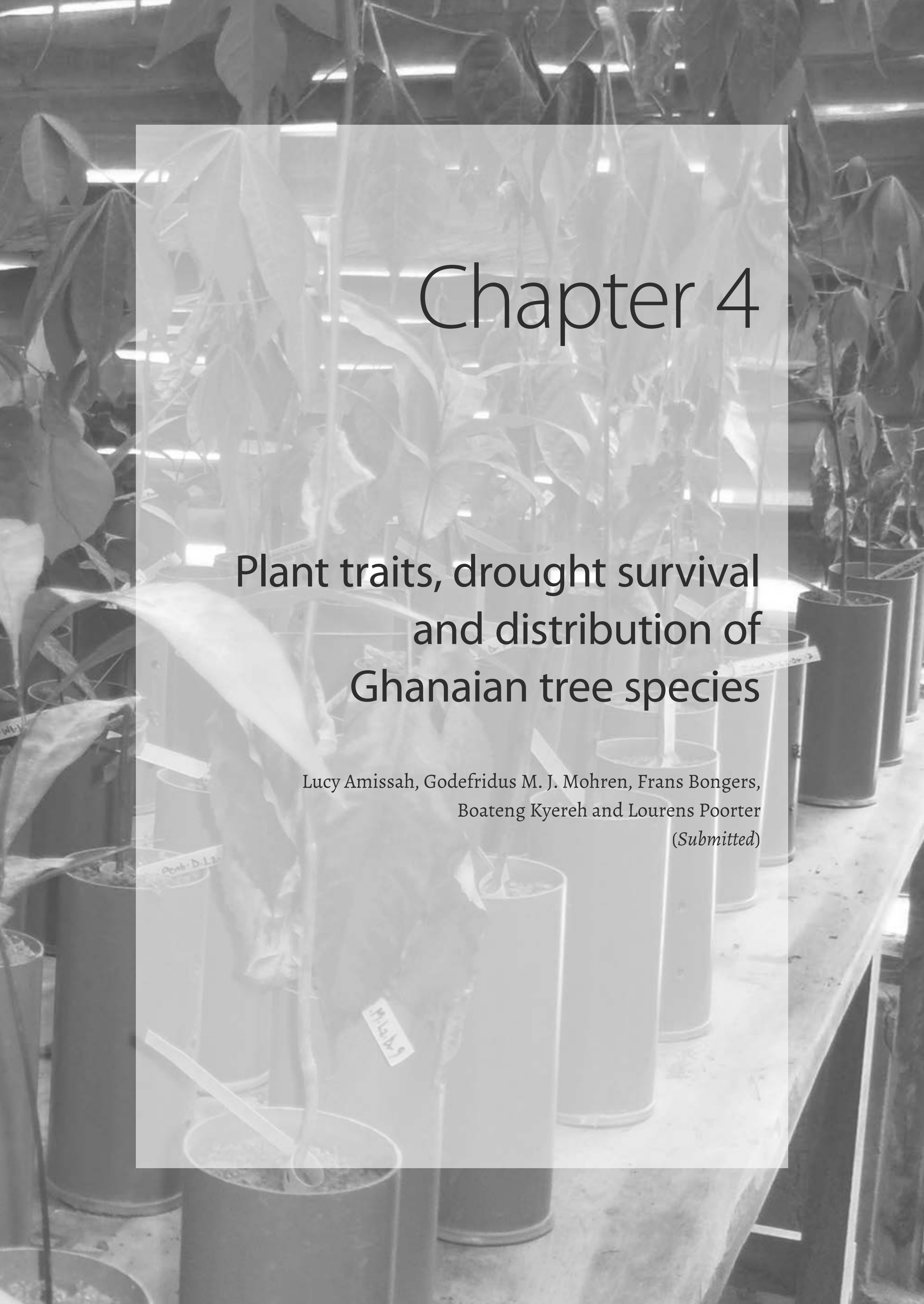
Appendix 1. Acidity and nutrient concentrations of moist forest soil used in the drought and shade experiment. Means and standard deviation are shown.

Acidity/Nutrients	Mean	Standard Dev.	indication
pH	6.5	0.28	neutral
Organic Carbon (%)	2.54	0.41	
Organic Matter (%)	4.38	0.03	moderate
Exchangeable Ca (meq/100g)	11.24	2.21	high
Exchangeable Mg (meq/100g)	3.26	1.057	low
Exchangeable K (meq/100g)	0.99	0.23	high
Cation Exchange Capacity (meq /100g)	15.67	3.56	moderate
Base Saturation (%)	99.33	0.17	high
Phosphorus (ppm)	7.44	1.18	low
Potassium (ppm)	128.61	23.97	high

Appendix 2. Temperature (°C) and relative humidity (%) in four greenhouses (High light 1 and 2 = 20% sunlight; Low light 1 and 2 = 5% sunlight) over the experimental period of three months including the four weeks that seedlings were conditioned in the greenhouses. Means and standard deviations are shown.

Greenhouse	Environmental variable	Mean	Standard deviation
High light 1	Temperature	28.07	1.61
	Relative humidity	75.90	7.30
High light 2	Temperature	27.82	1.52
	Relative humidity	76.19	6.77
Low light 1	Temperature	28.12	1.68
	Relative humidity	76.76	7.06
Low light 2	Temperature	27.90	1.49
	Relative humidity	77.27	6.41


R-hed
2.Dr.11



Chapter 4

Plant traits, drought survival and distribution of Ghanaian tree species

Lucy Amissah, Godefridus M. J. Mohren, Frans Bongers,
Boateng Kyereh and Lourens Poorter

(*Submitted*)

Abstract

Understanding the mechanisms underlying drought tolerance is important to understand current species distribution along the rainfall gradient, and to predict how species may respond to climate change. We evaluate the hypothesis that species show a trade-off between drought avoidance (deciduousness) and physiological drought tolerance (through construction of dense tissues), and a trade-off between rapid acquisition of resources versus the conservation of resources. We also tested the hypothesis that similar traits will predict drought survival and species position on the rainfall gradient. We studied 24 Ghanaian tree species with different distributions along the rainfall gradient in a greenhouse experiment where seedlings were exposed to two light treatments (5% and 20% of full sunlight) and two watering treatments (watered daily and water withheld for nine weeks). We measured 16 morphological and physiological traits and seedling growth and survival. In a separate analysis, we quantified the position of species on the rainfall gradient using climatic variables and inventory data of 2,505 1-ha plots distributed in the forest zone of Ghana. We found that species exhibited two main axes of strategy variation: (1) dense tissues and physiological drought tolerance versus drought avoidance and height expansion, and (2) resource acquisition versus resource conservation. Fast-growing species exhibited mostly a *drought avoidance* strategy whilst shade-tolerant species exhibited a *physiological drought tolerance* strategy. Drought survival was predicted by biomass allocation traits that enhance water uptake (high biomass fraction in roots) and reduce water loss (low biomass fraction in leaves) and by tough leaf- stem- and root tissues that enable physiological drought tolerance. Specific leaf area (leaf area per unit leaf mass) was the best predictor of the minimum rainfall at which species occurred; species with high SLA occurred at low rainfall. There was similarity in traits that predicted drought survival and species rainfall minimum. However, the most important traits were not the same, indicating that other factors than drought tolerance co-shape species distribution.

Our results suggests that trade-offs between drought avoidance versus physiological drought tolerance act in concert with other biotic and abiotic factors to determine species distribution along the rainfall gradient.

Key Words: drought tolerance, light availability, performance, plant strategies, rainfall gradient, resource acquisition and conservation, tropical forest, trade-off, water availability.

INTRODUCTION

Rainfall is one of the main factors determining species distribution and forest structure in lowland tropical forests (e.g. Bongers *et al.* 1999). Other factors, such as soil nutrients, light availability, herbivores and pathogens co-vary with the rainfall gradient and may affect species distribution as well (Davies *et al.* 2005, John *et al.* 2007, Sterck *et al.* in press). For example, high rainfall leads to strongly leached and nutrient-poor soils, and soil nutrients have been found to explain the distribution of apparent “wet” forest species (Swaine 1996, Condit *et al* 2013). With increasing rainfall the forest grows taller and denser (provided soil nutrients do not become limiting) resulting in shading and stronger competition for light. Fast height expansion is important to overtop neighbours and compete successfully for light, whereas species that regenerate in the shaded understory must be shade tolerant to be able to persist (Grubb 1998, Fonseca *et al.* 2000). Herbivore pressure also varies along the rainfall gradient; in Panama insect herbivore damage and herbivore mortality were higher in wet than in dry forest (Brenes-Arguedas *et al.* 2009).

Plant functional traits are the characteristics of plants that influence their growth, survival and reproduction and indirectly impact plant fitness (Violle *et al.* 2007). As a result plant functional traits may play a role in the partitioning of species along environmental gradients (Westoby & Wright 2006). Several studies have found a relationship between functional traits of species and species distribution across gradients in water availability (Maharjan *et al.* 2011), light availability (Poorter & Bongers 2006, Wright *et al.* 2010) and nutrient availability (Wright, Reich & Westoby 2001). Trade-offs between different traits contributes to the position of a species on resource gradients. Globally, a trade-off has been found between species from productive habitats that have rapid resource acquisition and fast growth, versus species from unproductive habitats that have high resource conservation and slow growth, but that survive very well (Wilson, Thompson & Hodgson 1999, Diaz *et al.* 2004, Kitajima & Poorter 2008).

Recent studies show that drought tolerance (i.e., the ability to survive under drought) is a strong predictor of the distribution of tropical tree species (Engelbrecht *et al.* 2007, Baltzer *et al.* 2008, Poorter & Makersteijn 2008). An understanding of the mechanisms underlying drought tolerance is important, as it allows the prediction of how species will respond to current (Malhi & Wright 2004, Phillips *et al.* 2008) and future increases in the frequency of drought (Sheffield &

Wood 2008). For example, Fauset *et al.*(2012) have shown that forest composition in Ghana has shifted in response to a drier climate in the past 20 years suggesting that climate change or drought in the form of inter annual variation in dry season intensity could have profound effect on forest composition and biomass. Plant species show three main strategies to deal with drought: (1) drought avoidance, (2) drought delay, and (3) physiological drought tolerance. These strategies are determined by a suite of morphological, physiological and phenological traits. Deciduous species *avoid* seasonal drought by shedding their leaves during the dry season, thus reducing water loss (Borchert 1994). Consequently, they have to maximize resource capture and growth during the shorter growing season. Most species exhibiting such a drought-avoiding strategy are long-lived pioneer species that construct cheap and thin leaves with high leaf area per unit dry mass invested (Givnish 2002, Markesteijn & Poorter 2009). Evergreen species *delay drought stress* by enhancing water uptake through deep roots, storing water in their roots and/or stem, and by reducing water loss through stomatal control (Quero *et al.* 2011). *Physiological drought tolerance* involves the ability to function physiologically even at low leaf water potential (Tyree *et al.* 2003, Kursar *et al.* 2009). Species with the capacity to tolerate low leaf water potentials are the ones with the lowest leaf water content (i.e., they have dense leaves). They also produce dense wood tissues (Searson *et al.* 2004, Markesteijn *et al.* 2011) to reduce the risk of cavitation and continue water transport during drought. As a result, these species also survive longest under dry conditions (Engelbrecht, Kusar & Tyree 2005, Poorter & Markesteijn 2008, Baltzer *et al.* 2008).

Light availability co-varies with the rainfall gradient and may contribute to the performance of species especially in the forest understorey (Veenendaal *et al.* 1996, Agyeman, Swaine & Thompson 1999, Brenes-Arguedas *et al.* 2011). Under conditions of high light and water availability plants perform well (growth and survival) but growth and survival are reduced under high light when water is limiting. Hence the interaction between light- and water availability may co-shape species distribution. Functional traits of plants growing in forest gaps and those in shaded environment may therefore contribute to plant performance and distribution. Only few studies have directly linked species position along the rainfall gradient (as quantified using plot data) with their traits as quantified from plants growing under optimal light environment (but see Engelbrecht *et al.* 2007, Markesteijn & Poorter 2008). Such an approach contributes not only to understanding individual species performance but also to the development of a mechanistic and predictive framework for species assembly in relation to resource gradients (Vesk 2013, Condit *et al.* 2013).

In this study we measured 14 morphological and four physiological traits for seedlings of 24 Ghanaian tree species growing under "optimal" growth conditions (20% of full sunlight and continuous watering) and in small gaps (5% of full sunlight and continuous watering). We determined species' drought survival in a dry-down experiment in which water was withheld, and related this to the species position along the rainfall gradient, which we quantified using 2505 temporary sample plots (Amissah *et al.* in press). We addressed three questions: First, how are species traits associated and what kind of plant strategies can be distinguished? We predicted that species show a trade-off between drought avoidance and drought tolerance, and a trade-off between resource acquisition and conservation. Second, which traits determine species drought survival and species distribution on the rainfall gradient? We predicted that species with a high drought survival, and species from low rainfall areas will have traits related to drought *delay*, such as increased water uptake (high biomass fraction in roots), high water storage (high root water content), and reduced transpirational water loss (i.e., low biomass fraction in leaves, specific leaf area and leaf area per unit plant mass). These species will also possess traits related to *physiological drought tolerance*, such as resistance to cavitation (through a high stem density) and the physiological ability to keep on functioning during drought (i.e., low leaf water potential and high leaf dry matter content). Third, is drought survival a good predictor of species position on the rainfall gradient? Do similar adaptations underlie species drought survival and distribution? We predicted that drought survival will correlate negatively with species position on the rainfall gradient and that similar traits will predict drought survival and species position on the rainfall gradient.

MATERIALS AND METHODS

Species selection

Twenty four tropical forest species from fourteen families were selected for the study (Table 1). The species had different distributions along the rainfall gradient in Ghana; 8 species from wet and moist forests, 11 species from dry forest, and 5 ubiquitous species that are found in both forest types. The species had also different light requirements for regeneration (pioneers, non-pioneer light demanders and shade tolerants; Hawthorne 1995). The species were selected because of their importance for timber trade in Ghana, their use as medicinal plants, and because of their different rainfall distributions. Seeds of the dry-forest species were collected from the dry forest (Afram Headwaters Forest Reserve), seeds of moist-forest species from the moist forest (Bobiri and Pra-Anum Forest Reserves) and seeds of the wet species were collected from the wet forest (Neung South and Subri Forest Reserves). In each forest reserve seeds were collected from 4-5 seed trees per species from January 2010 - June 2010. For the ubiquitous species two were collected from Afram Headwaters Forest Reserve and two from Bobiri Forest Reserve. To evaluate intraspecific adaptation, two genotypes of *Terminalia ivorensis* were collected from wet and dry forests. Seeds were transported to the laboratory of the Forestry Research Institute of Ghana (FORIG) in Kumasi and were germinated in germination trays at ca. 15% irradiance. Germinated seeds were then grown in polyvinyl chloride tubes (9 cm by 20 cm), filled with sandy loamy soils collected from the moist semi-deciduous forest (Bobiri Forest Reserve). Moist forest soil was used because of its texture (sandy loam soil) which allows for good drainage. In addition the pH and cation exchange capacity of the moist forests soil was about similar to that of the dry forest soils at levels sufficient for plant growth. Seedlings were grown for 3-4 months before being transferred to the greenhouses, where they were acclimated for four weeks before they were subjected to watering and no-watering treatments.

Table 1. List of species, abbreviations, family, guild, forest type and minimum annual rainfall ($R_{min,}$ in mm) at which species are found (based on species response curves). Species' family name, guild and forest types are according to Hawthorne (1995), Hawthorne & Jongkind (2006a), Hawthorne & Ntim Gyakari (2006b), and Hall & Swaine (1981). NPLD = Non-pioneer light demander. Abbrev. = Abbreviation, *Species without response curves. *Aningeria robusta* has been renamed *Pouteria aningeri.*

Species	Abbrev	Family	Species guild	Forest type	R_{min}
Heritiera utilis Sprague	Huti	Sterculiaceae	NPLD	Wet	1567
**Lophira alata* Banks ex Gaertn.	Lalt	Ochnaceae	Pioneer	Wet	
**Khaya ivorensis A. Chev.*	Kivo	Meliaceae	NPLD	Wet	
Pentadesma butyracea Sabine	Pbut	Caesalpinaceae	Shade tolerant	Wet	1630
Entandrophragma angolense (Welw).DC	Eang	Meliaceae	NPLD	Moist	1225
Turraeanthus africanus (Welw. ex C.DC.) Peller	Tafri	Meliaceae	Shade tolerant	Moist	1463
**Tieghemella heckelii* Pierre ex Chev	Theck	Sapotaceae	NPLD	Moist	
Terminalia ivorensis$_{Wet}$A.Chev.	Tivo$_{w}$	Combretaceae	Pioneer	Ubiquitous	1191
Piptadeniastrum africanum (Hook.f.) Brenan	Pafri	Mimosaceae	NPLD	Moist	1243
Ricinodendron heudelotii (Baill.) Pierre ex Pax	Rheu	Euphorbiaceae	Pioneer	Dry	1166
Newbouldia laevis (P.Beauv.) Seeman ex Bureau	Nivis	Bignoniaceae	Pioneer	Dry	1296
Mansonia altissima (A.Chev.) A.Chev.	Malt	Sterculiaceae	NPLD	Dry	1201
Nesogordonia papaverifera (Hook.f.) Brenan	Npapa	Sterculiaceae	Shade tolerant	Dry	1154
Ceiba pentandra (Linn.) Gaertn.	Cpent	Bombacaceae	NPLD	Dry	1148
*Celtis zenkeri Engl.	Czen	Ulmaceae	NPLD	Dry	
Albizia zygia (DC.) J.F. Macbr.	Azig	Mimosaceae	NPLD	Dry	1165
Pericopsis elata (Harms) Van Meeuwen	Prel	Papilionaceae	NPLD	Dry	1107
Sterculia rhinopetala K. Schum	Srhino	Sterculiaceae	NPLD	Dry	1166
**Khaya anthotheca* (Welw.) C. DC.	Kant	Meliaceae	NPLD	Dry	
**Aningeria robusta* *(Pouteria aningeri)* *(A. Chev.)Aubrev. and Pellegr.*	A rob	Sapotaceae	NPLD	Dry	
Antiaris toxicaria Leschenault	Atox	Moraceae	NPLD	Ubiquitous	1159
Strombosis pustulata J.Leonard	Sgla	Olacaceae	Shade tolerant	Ubiquitous	1207
Terminalia ivorensis A.Chev.	Tivo	Combretaceae	Pioneer	Ubiquitous	1191
Terminalia superba Engl. and Diels	Tsup	Combretaceae	Pioneer	Ubiquitous	1167

Dry-down experiment

A dry-down experiment was carried out in 4 greenhouses at FORIG (see Amissah *et al.* in prep. for a full description). The size of each greenhouse was 5.60 m x 4.96 m wide and 3 m high and inter-greenhouse distance was 4 m. A distance of 4 m was chosen so that neighbouring greenhouses would not shade each other. The greenhouses were aligned north-south to ensure that they all received the same amount of light at any point in time. Irradiance levels of 5% (two greenhouses) and 20% (two other greenhouses) were created by using bamboo slats, mosquito netting and raffia mats. The irradiance levels were determined through daily measurements in June 2010 with a light meter (Fisher Scientific Traceable Dual Display light meter, Fisher Scientific, Pittsburgh, USA) for 4 weeks. The 5% of irradiance is typical for small forest gaps, 20% of irradiance is typical for large forest gaps (Poorter & Rose 2005). As a minimum irradiance we used 5% rather than the 1%-2% of full irradiance that is typical for the forest understory, because many pioneer- and non-pioneer light demanding species were included in the study, and these would not have survived the understory light levels.

The experiment had a completely randomised factorial design with water, light and species as factors. Species were grown at two irradiance levels (5% and 20% of full light). For each species, 48-56 individuals were grown in each irradiance level except for two species *Pentadesma butyracea* and *Terminalia ivorensis* where 20 seedlings per species were used. Half (24-28) of the individuals of each species in each greenhouse received water, and the other half were not watered for nine weeks. We simulated therefore not continuous low water conditions, but the effect of a dry season drought. The positions of individual seedlings were rotated every two weeks in each greenhouse to ensure all species were exposed to the same environmental variation in the shade house. Because of limited seed availability and space constraints the experiment was conducted in two batches; the first was conducted from August-November 2010 and the second from February –May 2011. One species *(Ricinodendron heudelotii)* was included as a phytometer in both batches of the experiment to test for any systematic differences in the growing conditions in the greenhouses. Fourteen morphological traits calculated for *Ricinodendron heudelotii* individuals in the first and second batches of the experiment correlated strongly in both the 5% and 20% shade houses (5% light, Spearman $r = 0.99$, $P < 0.001$; 20% light, $r = 0.99$, $P < 0.001$). Additionally in a Principal Component Analysis of the same 14 traits the species in the two batches of the experiment occupied similar position in the traits space.

This indicates that the conditions in the shade houses were similar during the two batches of the experiment.

Seedling performance and traits measurements

Species performance and traits were measured under optimal growing conditions (20% of full light, well-watered plants) and low light conditions (5% of sunlight and well-watered plants). At the beginning of the experiment eight individuals were randomly selected for each species and their heights, diameters, leaf areas, stem and root lengths were measured and leaves counted. Sixteen individuals per species were selected for the final harvest for each light level and similarly measured as the initial harvest. Leaves were digitised with a desk-top scanner (Canon Lide 100) and leaf area was determined with pixel counting software Image J (Schneider, Rasband & Eliceiri 2012). Total root length was measured using the line intersect method (Newman 1966). Fresh weights of leaves, stems and roots were determined using a mass balance and the samples dried in an oven at 65°C for 48 hours. Relative growth rate was calculated for each species using initial and the final individual plant dry mass (at the end of nine weeks) with equation 1 (Hoffman & Poorter 2002).

$$\text{RGR plant dry mass} = (\overline{\text{lnPD2}} - (\overline{\text{lnPD1}}))/(t2 - t1) \qquad \text{Equation 1}$$

Where $\overline{\text{lnPD1}}$ and $\overline{\text{lnPD2}}$ are the means of natural logarithm transformed plant dry mass at time t_1 and t_2.

The basic measurements were used to calculate 14 seedling traits: leaf mass fraction (LMF; total leaf mass divided by plant mass, g g^{-1}), stem mass fraction (SMF, stem mass divided by plant mass, g g^{-1}), root mass fraction (RMF, root mass divided by plant mass, g g^{-1}), specific leaf area (SLA, leaf area per leaf mass, cm^2 g^{-1}), leaf area ratio (LAR, total leaf area divided by plant mass, cm^2 g^{-1}), specific stem length (SSL, stem length divided by stem mass, cm g^{-1}), stem length per unit plant mass (SLPM, stem length divided by plant mass, cm g^{-1}), specific root length (SRL, total root length divided by root mass, cm g^{-1}), root length per unit plant mass (RLPM, total root length divided by plant mass, cm g^{-1}), RLLA (root length per unit leaf area, cm cm-^{2}), leaf- stem- and root dry matter content (LDMC, SDMC and RDMC, dry mass per unit fresh mass x 100; %) and stem density (dry mass per unit stem volume; g cm^{-3}). The leaf traits (LMF, SLA, LAR) are important for light capture and transpirational water loss (Markesteijn &

Poorter 2009), the stem traits (SSL and SLPM) are important for light capture, water transport, stability and support (Poorter 1999). The root traits (RMF, SRL, RLPM and RLLA) are important for water capture, and for water storage (Poorter & Markesteijn 2008). Tissue dry matter content (LDMC, SDMC and RDMC) and stem density were calculated because they are related to physiological drought tolerance (Hacke *et al*. 2001, Jacobsen *et al*. 2005).

Assessment of survival and wilting, and physiological measurements

Seedling wilting stage and survival were assessed every week for a nine-week period. Seedling wilting stage was monitored following Tyree *et al.* (2002). Seedlings were ranked as slightly wilted if their leaves were green but leaf angle was slightly towards the ground compared to controls. Seedlings were considered nearly dead if most leaves were necrotic, with more extensive curling and leaf angles was mostly near 90° from horizontal with some young leaves still green near the midrib. Seedlings were considered to be dead if there were necrosis on all leaves, extensive curling, leaf blades brittle, and leaf angles mostly near 90° from horizontal. At the end of the experiment supposedly dead seedlings were watered again, to check whether they were really dead. None of the seedlings resprouted after watering. At the end of the experiment drought survival in the high light was quantified as the percentage of individuals alive in the dry treatment relative to the number of individuals at the beginning of the experiment. Drought survival in the low light treatment was quantified similarly. Mortality in the continuously watered treatment was negligible.

Mid-day leaf water potential was measured on six slightly wilted and nearly dead individuals (as indicator of lethal water potential) of each species in each greenhouse using the pressure bomb technique (Tyree & Hammel, 1972). Leaf water potential was measured because it gives an indication of the level of water stress within a plant and its physiological drought tolerance (Tyree *et al.* 2002).

Species response curves

Species response curves to rainfall were created independently (Amissah *et al.* in press) for 18 out of our 24 species (Table 1), using 2505 inventory plots that covered most of the forest gradient in Ghana (Hawthorne 1995, Hawthorne & Abu Juam 1995, Hawthorne 1996). Within forest reserves, a systematic 2 x 2 km grid was established, and 1-ha plots were established at each grid intersection. Trees

≥ 30 cm diameter at breast height (dbh) were inventoried over the entire plot, trees 10-30 cm dbh were identified in 0.1 ha subplots, and trees 5-10 cm dbh were identified in 0.05 ha subplots. For this analysis we used presence/absence data because species abundance is affected by a wide range of other processes such as competition, and recovery from past disturbance (Toledo *et al*. 2012).

To analyze species responses to the environmental conditions and to construct individual species response curve to rainfall a forward multiple logistic regression analysis was conducted for the presence/absence of a species on the four climatic variables: annual rainfall, rainfall seasonality, isothermality and temperature seasonality as derived from Worldclim data base (Hijman *et al.* 2005). To be able to model bell-shaped responses both the simple and quadratic terms were included (see Amissah *et al*. in press for more details).We constructed the response curves to annual rainfall for each species while keeping the other three climatic factors constant. Species rainfall minimum (R_{min}), optimum (R_{opt}), maximum (R_{max}) and range (R_{range}) were derived from the species rainfall response curves. Rainfall optimum was the value at which species occurrence reached the maximum. R_{min} and R_{max} were calculated as rainfall at the 10th percentile and rainfall at the 90th percentile of the probability of occurrence (Maharjan *et al.* 2011). R_{range} was calculated as the difference between R_{min} and R_{max}. R_{mim} and R_{opt} were significantly positively correlated ($r = 0.66$, $P \leq 0.001$, $n = 18$) and R_{max} and R_{opt} as well ($r = 0.50$, $P \leq 0.05$, $n = 18$). Based on these correlations R_{min} was used for further analysis. This is because R_{min} indicates the lowest annual rainfall at which a species can occur. At this rainfall minimum water availability may be a bottleneck for plants survival and growth.

Data analysis

A Kaplan Meier survival analysis (Log-Rank test) was conducted to test whether the 24 species differed in their survival time in response to experimental drought. In this analysis median survival time was calculated for only 18 species because in six of the species more than 50% of the seedlings were alive at the end of the experiment. Species that were taller at the start of the experiment could show a different drought survival because they transpire more and deplete soil water more rapidly, or because they have a larger root system and a better access to soil water (Lopez-Iglesias, Villar & Poorter 2014). To control for the effect of size on drought survival, the average height, diameter and number of leaves for the species at the start of the experiment were used as covariates in a Cox regression

(Forward Log likelihood). An ANCOVA analysis was performed to evaluate the effects of light and water on morphological traits including plant dry mass as a covariate to correct for effects of seedling size and ontogenetic drift. Values of SLA, LAR, RLLA, SSL, SRL, SLPM, RL and SD were $\log_{10}$ transformed, whereas values of LMF, SMF, RMF, LDMC, SDMC and RDMC were arcsine transformed before they were used in the ANCOVA analysis. Size-corrected species mean trait values generated from the ANCOVA analysis (i.e., predicted trait values at a common biomass of 6.3 g) was used in all further analyses.

We evaluated association among 18 species traits (of seedlings growing under 20% and 5% of full sunlight and receiving continuous watering) and relative growth rate using Principal Component (PCA) analysis with varimax rotation. We tested the combination of seedling traits that could best predict seedling drought survival with a multiple regression. We used a regression modeling averaging approach (Spatial Analysis in Macroecology, SAM version 4, Rangel, Diniz-Filho & Bini 2010) because it allowed for all possible combinations of all predictors and selection of the best model based on Akaike information criterion (AIC). The AIC gives an indication of how models best fit the observed data. Parameter estimates are also averaged across all generated models (1023 OLS (ordinary least square) models), using Akaike Weights (AICc wi), which is the relative likelihood of the model given the data (Johnson & Omland 2004). The contribution of individual variables to the selected models is also indicated by importance values. The closer the importance value to 1 the more important the variable. For the multiple regression, 10 morphological and physiological traits: LMF, LDMC, SLA, RLLA, SRL, RMF, RDMC, SD and leaf water potential at slightly wilted and at moribund stage (nearly dead stage) were used as predictors and survival at seven weeks (under 5% and 20% sunlight and no watering) as dependent variable. Ideally, we should have used the median drought survival time as our response variable, but because not all species had shown 50% mortality by the end of the 9 weeks experiment, we used the percentage of drought survival at 7 weeks. We used seven weeks as our reference, because at that moment the species showed the largest variation in drought survival (4% -100%) in the high light treatment. We also evaluated in a regression analysis the combination of plant traits that predict minimum annual rainfall (R_{min}) at which species are found for the 18 species for which rainfall response curves were available. Traits of seedlings growing under the 20% full sunlight were used in the analysis because it reflects the full potential of plant traits under “optimal” growth conditions. The low light traits explained very little of the variation in drought survival (Appendix 1). All other statistical analyses were conducted using IBM SPSS statistics for Windows version 19.0 (IBM Corporation, Armonk, New York).

RESULTS

Trait associations

The first Principal Component Analysis (PCA) axis explained 31% of the variation in species traits and was associated with species physiological drought tolerance (LWP at slightly wilted and nearly dead stages) and tissue density (LDMC, SDMC and SD) at the right of the axis and deciduousness and potential for height expansion (SLPM, SSL, and SMF) at the left of the axis (Fig. 1). Moist and dry forest species did not have a different loading on the first axis (test, t = -0.044, df = 17, P = 0.96). However, species that differ in shade tolerance loaded significantly different on the first axis (t-test, t = 3.20, df = 24, P = 0.004), with pioneers (such as *Ceiba pentandra* and *Ricinodendron heudelotii*) on the left versus shade tolerant and non-pioneer light demanders species on the right. The second PCA axis explained 22% of variation in species traits and was associated with traits that facilitate aboveground (LAR, SLA) and belowground (SRL and RLPM) resource capture and fast growth (RGR). Pioneers had significantly higher loadings on this axis compared to shade tolerant and non-pioneer light demanders (t- test, t = -2.56, df = 22, P = 0.02). Species with acquisitive traits and high relative growth rate are found on top (e.g., *Terminalia superba* and *Terminalia ivorensis*) whereas species with conservative traits and slow relative growth rate are found at the bottom of the axis *(e.g Pentadesma butyracea* and *Turraeanthus africanus)*. Similarly, dry species *(e.g., Pericopsis elata and Khaya anthotheca*) were at the top, and wet/moist (*Heritiera utilis and Tieghemella heckelii)* were at the bottom of this axis (t-test, t = 2.54, df = 17, P = 0.02). Correlations among species traits and the first and second PCA axes are found in Table 2.

Table 2. Correlation among species traits, drought survival at week 7, species position along rainfall gradient and the first two PCA axes of 24 tree species. Traits were calculated at a standard seedling size of 6.3 g. Pearson correlation coefficient are shown, 2-tailed, n = 24, for traits and n = 18 for species distribution at (**bold**), $P \leq 0.05$, (**Bold + *italics***) $P \leq 0.01$, (**Bold + underline**) **P** ≤ 0.001

	LMF	LDMC	SLA	LAR	SMF	SD	SDMC	SSL	SLPM	RMF	RDMC	SRL	RLLA	RLPM	LWP$_{swDry}$	LWP$_{swWet}$	LWP$_{ndDry}$	LWP$_{nsWet}$	RGR	SV$_{wk7}$	R$_{min}$	R$_{max}$	R$_{opt}$	R$_{med}$	R$_{range}$
LMF																									
LDMC	0.05																								
SLA	-0.06	-0.39																							
LAR	0.12	-0.15	**0.82**																						
SMF	***0.57***	**-0.49**	0.28	0.09																					
SD	0.18	***0.54***	-0.05	-0.07	-0.06																				
SDMC	0.06	**0.70**	-0.30	-0.04	**-0.43**	**0.61**																			
SSL	-0.19	-0.23	0.30	0.21	-0.10	***-0.54***	**-0.43**																		
SLPM	0.09	**-0.73**	**0.43**	0.18	**0.72**	**-0.40**	**-0.72**	0.39																	
RMF	***0.54***	0.22	-0.20	-0.36	-0.17	0.17	0.05	0.03	**-0.16**																
RDMC	-0..03	**0.60**	0.16	0.37	-0.34	***0.56***	**0.68**	-0.03	**-0.34**	-0.13															
SRL	0.17	-0.25	***0.60***	***0.53***	0.35	0.35	**-0.43**	0.05	**0.35**	-0.17	0.22														
RLLA	**0.49**	0.00	0.06	-0.04	**0.42**	0.14	-0.10	-0.08	**0.13**	**0.47**	-0.01	**0.65**													
RLPM	0.07	-0.12	***0.56***	***0.50***	0.14	0.02	-0.15	0.14	**0.18**	-0.07	0.24	**0.94**	**0.69**												
LWP$_{swDry}$	-0.15	***0.52***	-0.02	0.19	-0.43	***0.56***	***0.53***	-0.33	**-0.65**	0.04	**0.42**	-0.20	-0.23	-0.11											
LWP$_{swWet}$	0.01	**0.45**	-0.12	0.03	**-0.44**	0.31	**0.44**	-0.16	**-0.71**	0.22	0.19	-0.35	-0.20	-0.21	**0.84**										
LWP$_{ndDry}$	0.06	***0.56***	-0.02	0.19	**-0.39**	**0.42**	***0.53***	-0.28	**-0.68**	0.07	0.34	-0.25	-0.27	-0.18	**0.69**	**0.67**									
LWP$_{nsWet}$	0.03	**0.44**	-0.22	-0.04	-0.33	0.23	**0.40**	-0.25	**-0.59**	0.08	0.20	**-0.39**	-0.28	-0.35	**0.66**	**0.73**	**0.74**								
RGR	0.25	0.36	**0.79**	**0.71**	**0.42**	0.08	0.30	0.18	0.38	-0.04	0.04	**0.44**	0.15	**0.40**	0.06	0.02	0.02	0.00							
SV$_{wk7}$	-0.13	0.31	-0.17	***-0.42***	0.04	0.32	0.04	-0.28	**-0.19**	0.30	-0.15	-0.20	-0.12	-0.16	0.04	-0.03	0.05	0.00	-0.19						
R$_{min}$	-0.27	0.12	***-0.66***	***-0.60***	-0.33	-0.15	0.13	-0.23	**-0.02**	0.20	-0.02	-0.20	-0.04	-0.22	-0.17	-0.20	-0.22	-0.13	**-0.60**	-0.09					
R$_{max}$	-0.07	0.24	***-0.58***	***-0.58***	-0.22	0.14	0.08	0.04	**-0.28**	0.14	0.08	-0.17	0.09	-0.17	-0.23	-0.20	-0.22	-0.09	***-0.56***	0.19	0.43				
R$_{opt}$	-0.14	0.19	***-0.57***	***-0.49***	-0.38	0.14	0.21	-0.20	**-0.20**	-0.24	0.07	-0.03	-0.07	-0.01	0.01	0.00	-0.21	-0.19	***-0.45***	0.00	***0.66***	**0.50**			
R$_{med}$	0.03	0.31	-0.42	-0.04	-0.07	0.22	0.34	-0.26	**-0.22**	0.13	0.08	-0.36	-0.09	-0.41	0.13	0.10	0.39	0.36	-0.33	0.25	0.42	0.32	0.12		
R$_{range}$	-0.16	0.13	0.00	0.15	0.08	0.28	-0.03	0.25	**0.14**	0.32	0.11	0.00	0.13	0.02	-0.07	-0.02	-0.05	0.19	-0.03	0.27	-0.45	**0.61**	-0.08	-0.05	
PCA axis 1	0.01	**0.77**	-0.12	0.15	***-0.53***	**0.68**	**0.80**	***-0.35***	**-0.83**	0.07	**0.64**	-0.18	-0.14	-0.08	**0.86**	**0.77**	**0.82**	**0.69**	-0.09	0.07					
PCA axis 2	0.26	-0.20	0.81	**0.81**	0.37	0.19	-0.12	0.11	0.33	-0.11	0.34	0.86	0.47	0.82	0.02	-0.22	-0.03	-0.26	0.79	-0.23					

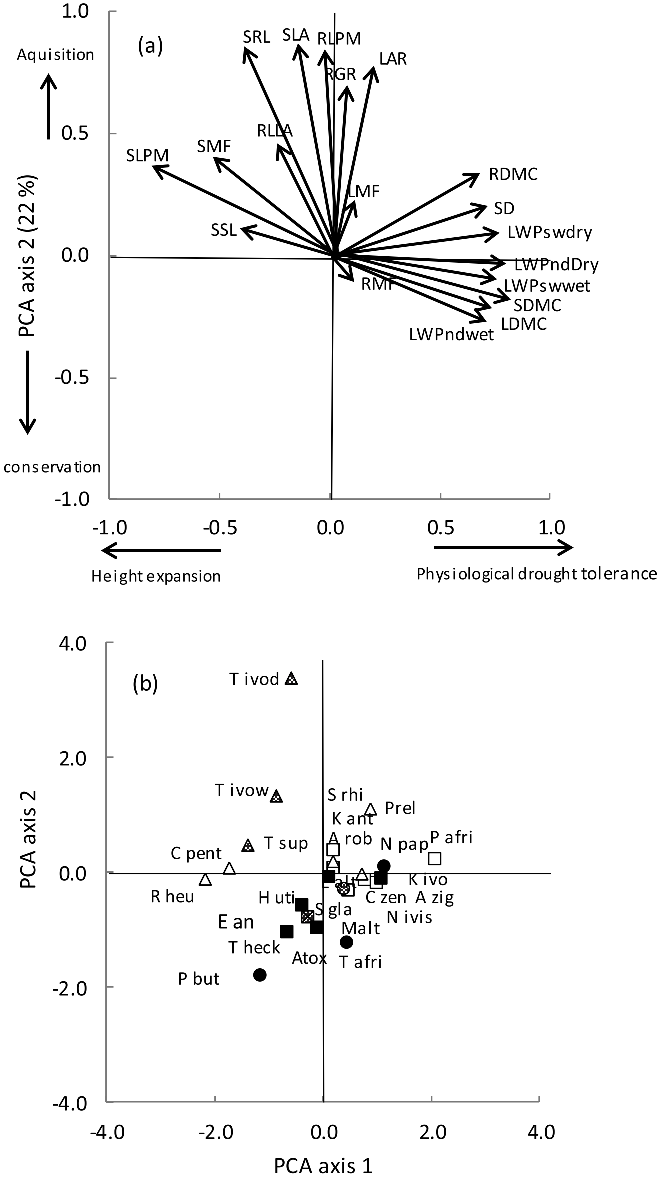


Figure 1. Principal Component Analysis plot showing, (a) the loadings of morphological, physiological and growth-related seedling traits, and (b) loadings of 24 Ghanaian tree species on the multivariate traits space. Trait values were calculated at a standardised seedling size of 6.3 g. For species abbreviations see Table 1. Species differed in the forest type in which they are most abundant (wet- and moist-forest species = black; ubiquitous species = dotted, dry-forest species = white) and their shade-tolerance (pioneer = triangle, non-pioneer light demander = square and shade tolerant = circle). Leaf water potentials (LWP) were determined for seedlings growing under 20% irradiance under droughted conditions and the other traits were determined for seedlings growing under "optimal" conditions (20% irradiance, watered). For trait abbreviations, see the methods.

Seedling traits and drought survival

Species differed significantly in their survival time (Log Rank, Chi-Square = 777.4, df = 23, P = 0.001, Fig. 2). The first seedlings started to die after three weeks. Drought survival at seven weeks varied from 100% for *Albizia zygia* to 4% for *Terminalia superba*. A series of multiple regression analysis was done, relating drought survival to the underlying seedling traits. The global model selected six traits (LMF, SLA, RMF, LDMC, RDMC and SD) and explained 64% of the variation in species survival (Table 3). Leaf mass fraction (Fig. 3a) was the most important variable (Importance = 0.98) and was significantly negatively related to drought survival. LDMC was as important as LMF (Importance = 0.97) and was significantly and positively related to drought survival (Fig. 3c). Both RMF (Fig. 3b) and RDMC (Table 3) were significantly negatively related to survival. Stem density (Fig. 3d) and SLA were positively related to drought survival in the global multiple regression model (Table 3), although individually, SLA showed a negative bivariate relationship with drought survival (Fig. 3e). None of the physiological traits (Leaf water potential at slightly wilted and nearly dead stage) included in the analysis significantly predicted drought survival (Table 3). Leaf area ratio was not included as a predictor in the model to reduce multi-collinearity; however the bivariate relation showed that drought survival decreased with leaf area ratio (Fig. 3f).

Table 3. Regression models fitted for traits of species, drought survival after 7 weeks and species annual rainfall minimum (R_{min}). The importance of traits and their coefficients (Beta) are shown. Significant traits are shown in bold based on 95% confidence interval. The R^2 for the fitted model for drought survival and traits is 0.64 (n = 24) and that for fitted model for species annual rainfall minimum is 0.30 (n = 18). See text for traits abbreviation.

Traits	Drought survival		R_{min}	
	Importance	Beta	Importance	Beta
LMF	0.98	**-0.68**	0.15	**-0.15**
LDMC	0.97	**0.82**	0.18	**-0.26**
RDMC	0.66	**-0.46**	0.19	**0.26**
RMF	0.47	**-0.34**	0.12	-0.04
SD	0.26	**0.22**	0.12	-0.04
SLA	0.20	**0.17**	0.97	**-0.74**
SRL	0.15	0.07	0.22	**0.27**
LWP_{ndDry}	0.13	0.04	0.20	**-0.23**
RLLA	0.13	0.01	0.16	**0.15**
LWP_{swDry}	0.13	0.02	0.17	**-0.19**

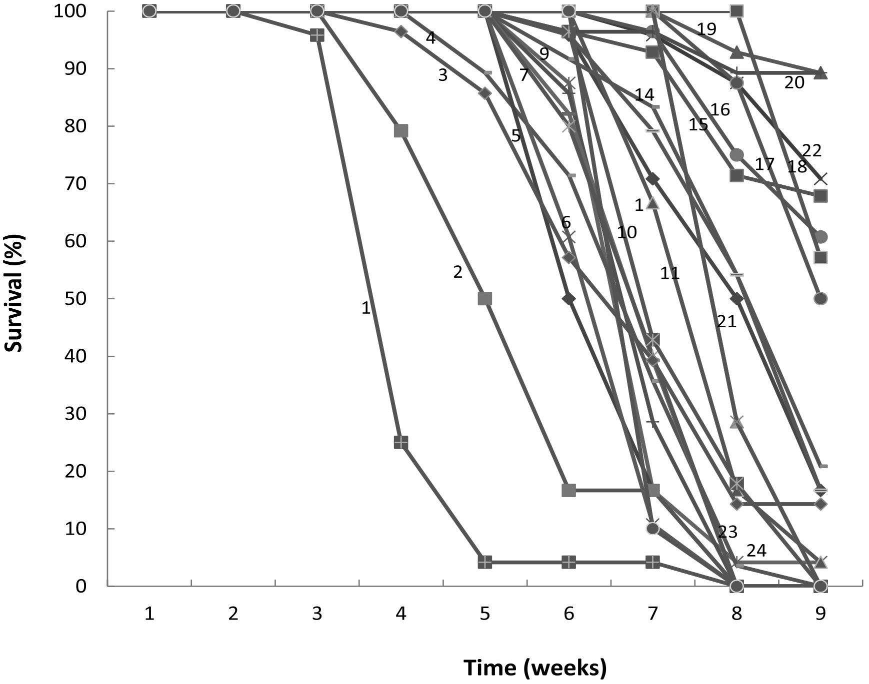


Figure 2. Survival curves of seedlings of 24 Ghanaian forest species exposed to nine-week experimental drought in 20% full sunlight. Number of seedlings n = 24- 28 per species. For two species (*Pentadesma butyracea* and the wet genotype of *Terminalia ivorensis*) 10 seedlings per species were used. 1 = *Terminalia superba*, 2 = *Mansonia altissima*, 3 = *Sterculia rhinoptela*, 4 = *Khaya ivorensis*, 5 = *Lophira alata*, 6 = *Nesogordonia papaverifera*, 7 = *Pentadesma butyracea*,8 = *Ricinodendron heudelotii*, 9 = *Heritiera utilis*, 10 = *Terminalia ivorensis (wet genotype)*,11 = *Terminalia ivorensis (dry genotype)*,12 = *Newbouldia laevis*, 13 = *Antiaris toxicaria*, 14 = *Strombosia pustulata*, 15 = *Pouteria aningeri*, 16 = *Piptadeniastrum africanum*, 17 = *Entandrophragma angolense*, 18 = *Turraeanthus africanus*, 19 = *Albizia zygia*, 20 = *Pericopsis elata*, 21 = *Tieghemella heckelii*, 22 = *Ceiba pentandra*, 23 = *Khaya anthotheca*, 24 = *Celtis zenkeri*.

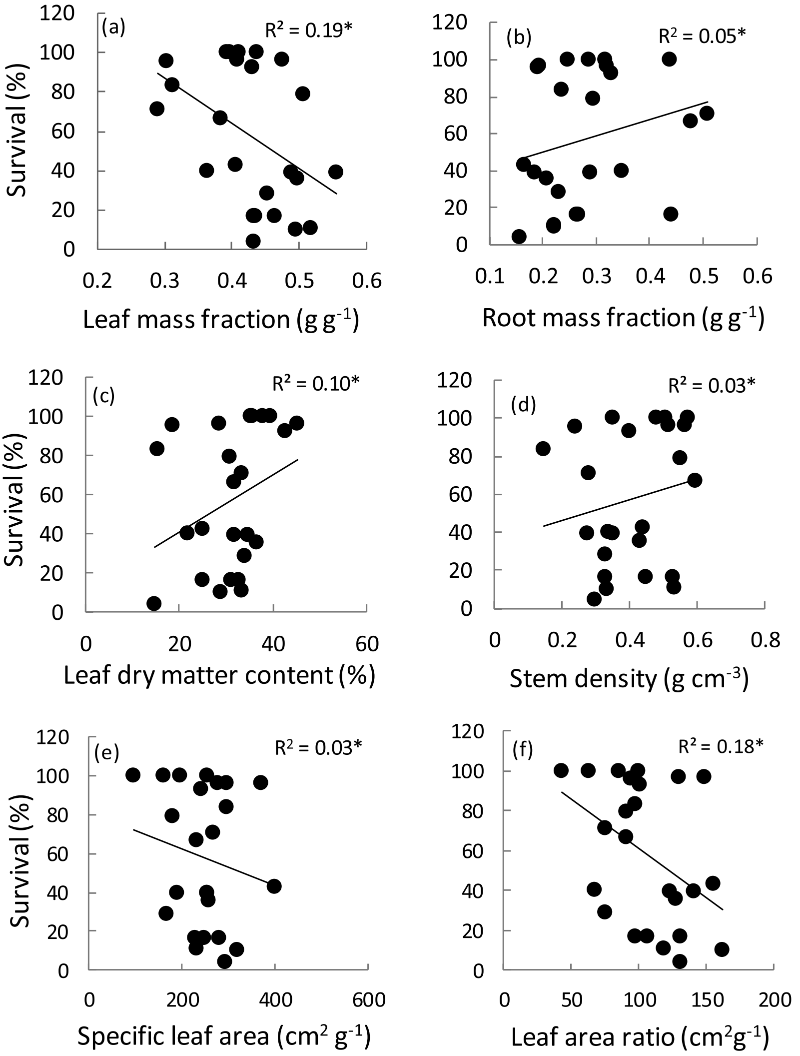


Figure 3. Relation between drought survival of seedlings of 24 Ghanaian tree species and their traits under optimal growth conditions. (a) Leaf mass fraction, (b) root mass fraction, (c) leaf dry matter content, (d) stem density, (e) specific leaf area and (f) leaf area ratio. Regression lines, coefficients of determination (R^2) and significance levels are shown. * $P < 0.05$.

Seedling traits and species distribution

Specific leaf area was the most important variable predicting species distribution at minimum annual rainfall and had an importance value of 0.97 over all variables in the regression models. Species with high SLA could persist in drier areas and had low rainfall minimum (Fig. 4a). The other significant variables had a much lower importance (0.15-0.22; Table 3). LMF, LDMC and leaf water potential at the slightly wilted and nearly dead stage were negatively associated with species rainfall minimum (Table 3, Fig. 4a) whereas RDMC, SRL and RLLA were positively associated with species rainfall minimum (Table 3). Leaf area ratio was negatively related to rainfall minimum (Fig. 4b). Drought survival was not significantly related to any aspect of species distribution on the rainfall gradient (Fig. 4d).

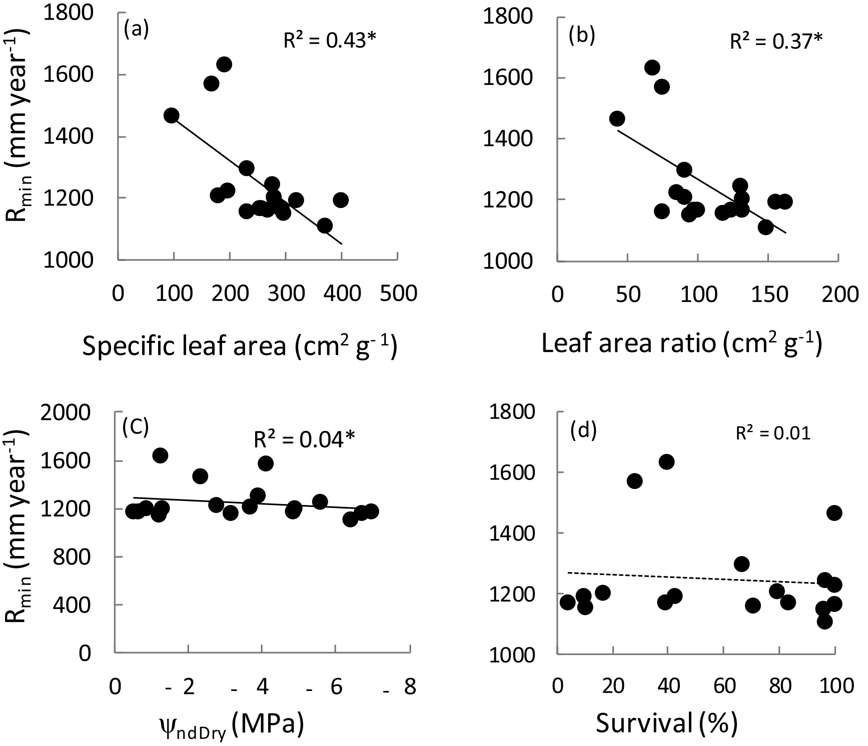


Figure 4. Relationship between the minimum rainfall (R_{min}) at which 18 Ghanaian tree species occur, and their (a) specific leaf area (SLA), (b) leaf area ratio (LAR), (c) mid-day leaf water potential at nearly dead stage (ψ_{ndDry}) and (d) drought survival. SLA and LAR were determined for well-watered seedlings, leaf water potential was determined for droughted seedlings. Regression lines, coefficients of determination (R^2) and significance levels are shown. * $P < 0.05$; ** $P < 0.01$. Significant regressions are shown with continuous lines, non-significant regressions with broken lines.

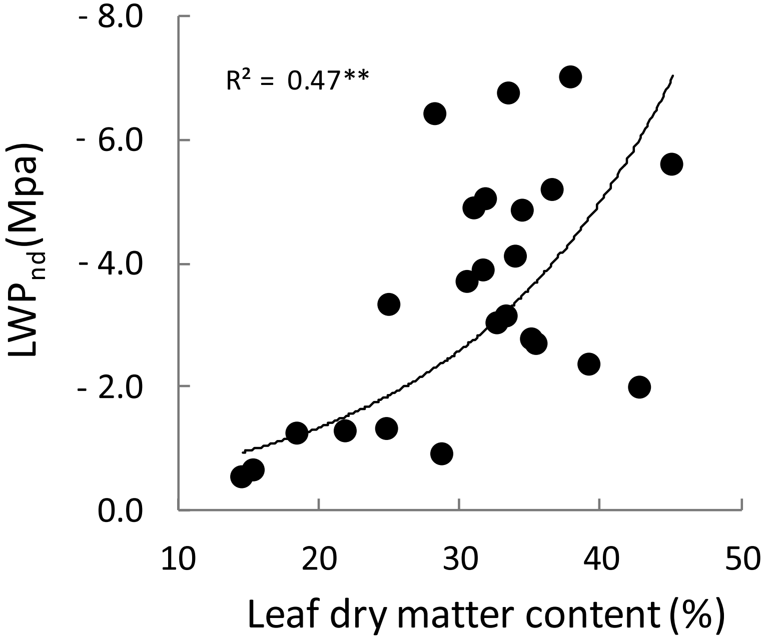


Figure 5. Relationship between mid-day leaf water potential of nearly dead plants (LWP_{nd}) and leaf dry matter content of seedlings of 24 Ghanaian tree species. Regression line, coefficient of determination (R^2) and significance level are shown. ** $P < 0.01$.

DISCUSSION

We evaluated how physiological and morphological functional traits are associated and identified plant strategies related to drought tolerance and resource capture and conservation. Two main axes of strategy variation were identified (1) dense tissues and physiological drought tolerance versus drought avoidance and height expansion and (2) resource acquisition versus resource conservation confirming the basic assumption as indicated in the introduction. We also determined traits that predict drought survival and species distribution in a separate analysis and found that drought survival was predicted by a suite of traits related to biomass allocation and tissue density. There was an overlap in traits that predicted drought survival and those that predicted species distribution at annual rainfall minimum but the most important traits did not overlap, which suggests that other factors than drought tolerance may co-shape species distribution along the rainfall gradient.

Trait associations and plant strategies

We hypothesised that species would show a trade-off between drought avoidance and drought tolerance, and a trade-off between resource acquisition and conservation. Our results confirmed our predictions as we indeed identified two main axes of variation (1) dense tissues and physiological drought tolerance at the right side of the axis and drought avoidance and height expansion at the left side of the axis and (2) resource acquisition versus resource conservation (Fig. 1a). Drought avoidance is the ability of a plant to shed its leaves at the onset of the dry season to prevent desiccation whereas physiological tolerance is the ability of plants to continue physiological functioning (e.g. hydraulic conductance) at low leaf water potential (Baltzer *et al.* 2008, Kursar *et al.* 2009). Dry and wet forest species did not occupy significantly different positions on the first axis but pioneer species with deciduous habit occupied the drought- avoiding side of the axis and non-pioneer light demanders and shade bearers occupied the physiological drought tolerance side of this axis (Fig. 1b). Shade-tolerant species tend to possess physiological drought tolerance traits, indicating that shade tolerance and drought tolerance might be coupled (cf. Markesteijn *et al.* 2011) which contrasts with the widely established idea that there should be a trade-off between shade- and drought tolerance (Smith & Huston 1989). Our findings suggest that shade tolerant species are likely to have the capacity to tolerate drought stress.

The first axis reflects a trade-off between maximising water transport and a deciduous leaf habit, versus minimizing the risk of xylem embolism (Jacobsen *et al.* 2007, Pratt *et al.* 2007, Meinzer *et al.* 2008). The drought avoidance strategy is controlled by deciduousness, which is typical for dry forest species. Deciduousness has been associated with high hydraulic efficiency and a high risk of cavitation (Méndez-Alonzo *et al.* 2012). The trade-off on the first axis between efficient height expansions versus dense tissues may be because a low wood density allows species to realize an efficient height expansion per unit plant biomass invested (Iida *et al.* 2012) and a fast growth (Kitajima 1994, Muller-Landau 2004). Additionally low wood density implies lower volumetric construction cost, higher hydraulic conductance and, as a result, higher photosynthetic rates (cf. Chave *et al.* 2009).

The second axis represented a trade-off between acquisitive species (pioneers and dry forest species) at the top and conservative species (non-pioneers and wetter species) at the bottom. Acquisitive species have a large potential to capture resources, both aboveground (light) by investing in a large leaf area, and belowground (water, nutrients) by investing in a large root system (Fig. 1). Consequently these acquisitive species realize fast relative growth rates. This trade-off between resource acquisition and resource conservation is consistent with the findings of many studies on temperate and tropical species (Grime *et al.* 1997, Wilson *et al.* 1999, Kitajima & Poorter 2008). Generally a conservative resource strategy prevails in a resource-poor environment whereas rapid rate of resource acquisition prevails in a resource-rich environment (Grime 1979, Grime *et al.* 1997, Wilson *et al.* 1999). Moist and wet forest species were more conservative in their resource use than dry forest species probably because they are adapted to the low light environment and low carbon gain in wetter forest. The dry forest species that we included in our study may have an acquisitive strategy to grow rapidly in the shorter growing season (Grubb 1998, Fonseca *et al.* 2000). This should especially be the case for the deciduous species. At even lower rainfall levels more conservative species can be found, that are evergreen and conserve water, carbon, and nutrients (Wright & Westoby 2002, Givnish 2002).

Drought survival and associated traits

Six traits significantly contributed to species variation in drought survival, indicating that a suite of traits contributes to a drought tolerance strategy. These traits were associated with biomass allocation (LMF and RMF), leaf display (SLA) and tissue density (LDMC, RDMC and SD). We predicted that high drought survival would be associated with traits related to drought delay, such as increased water uptake (high root mass fraction), high water storage (high root water content), and lower water loss due to transpiration (i.e., by having low leaf mass fraction, specific leaf area and leaf area ratio). We indeed found that drought survival was positively related to root mass fraction and root water content, and negatively related to LMF (Table 3), indicating that *drought delay* is an important component of a drought survival strategy (cf Tyree *et al.* 2003).

We also predicted that drought survival would be related to physiological drought tolerance, such as low leaf water potential, high leaf dry matter content, and cavitation resistance (through a high stem density). Drought survival was indeed strongly related to leaf dry matter content, as indicated by the high importance value (0.97). High LDMC implies structurally reinforced and dense leaves. Such leaves have a high modulus of elasticity, which enables them to decrease their leaf water potentials to very low and negative values (Niinemets

2001). Indeed, in our study we found a moderate positive correlation between LDMC and the LWP under the slightly wilted ($r = 0.52$, $P \leq 0.01$, $n = 24$), and nearly dead stage ($r = 0.56$, $P \leq 0.01$, $n = 22$, Fig. 5). Strangely enough, LWP itself was not significant in the multiple regression model (Table 3), despite the fact that it has been found to be a good predictor for drought survival in other studies (Baltzer *et al.* 2008, Kursar *et al.* 2009).

Drought survival was positively related to stem density. Plants with higher stem density are able to resist cavitation (Jacobsen *et al.* 2007, Markesteijn *et al.* 2011, Méndez-Alonzo *et al.* 2012), probably because of a combination of narrow vessels and small pit pores which reduces the chance of embolism (Lens *et al.* 2013), and of structurally reinforced vessels that reduce the chance of vessel implosion (Hacke *et al.* 2006, Jacobsen *et al.* 2007). Overall, these results suggest that *physiological drought tolerance* and its associated structural traits is an additional component of a drought survival strategy.

Traits and species distribution

Plant functional traits are important for plant performance and hence for species distribution (Westoby & Wright 2006). Traits may set the lower (R_{min}) or upper (R_{max}) limit where a species occurs, or they may determine where a species performs at it maximum (R_{opt}). As we focused on drought tolerance, we expected traits to be related to the lower limits of rainfall where a species is found. We predicted that species with a low minimum annual rainfall distribution (low R_{min}) would have traits that delay drought and indicate high physiological drought tolerance.

The multiple regression model showed that eight traits were significantly related to species distribution. SLA was the single best predictor of species' rainfall distribution (R_{min}), with an importance value of 0.97 (Table 3). It has been reported that SLA strongly decreases with increasing drought to reduce transpiration (Carter, Theodorou & Morris 1997, Milla *et al.* 2008, Poorter 2009). Because seasonal drought is more prevalent in dry forests than in wet forests, we expected a low SLA for dry species. Instead, we found that dry species had a higher SLA. This observation could be related to a drought avoidance strategy; most deciduous species have high SLA for rapid growth during the short growing season (Ruiz-Robleto &Villar 2005). However, given the fact that we had only 4 deciduous species in our study, this cannot explain the overall pattern of SLA association with species rainfall minimum. Most likely, the observed pattern is not driven by water availability and drought, but by other factors that co-vary along the rainfall gradient; with an increase in annual rainfall there is an increase in pest pressure, and a decrease in light and nutrient availability (due to leaching of soil). Species from high rainfall forests may produce thick and dense leaves with low SLA to escape attacks from herbivores and pathogens (Kitajima & Poorter 2010). At the same time, such well-protected leaves have an increased leaf lifespan, which allows plants to pay back the initial construction cost of the leaves, enhance the carbon and nutrient residence time in the plant, and hence, plant performance in shaded and nutrient-poor environments. Other studies have also found that low SLA is closely linked to shade tolerance (Kitajima 1994, Poorter & Bongers 2006), nutrient tolerance (Aerts 1999, Baltzer & Thomas 2010) and drought tolerance (Erice 2010). SLA is one of the major traits contributing to the 'primary axis of specialization' (Grime *et al.* 1997) and the global leaf economics spectrum (Wright *et al.* 2004), and determines species distribution along a nutrient gradient (Phillips *et al.* 2003), water gradient (Bongers *et al.* 1999, Ackerly 2004), and light gradient (Ackerly *et al.* 2002) at large spatial scales, and at large temporal scales during secondary succession (Krober *et al.* 2012, Lohbeck *et al.* 2013). The other traits that significantly explained the rainfall distribution (R_{min}) of the species had much lower importance values (0.15-0.22, Table 3). Three of these traits (LMF, LDMC and RDMC) also explained drought survival and may suggest similar mechanisms involved in drought survival and species distribution in low rainfall areas. According to the regression model, species from wetter environments (higher R_{min}) had higher SRL and RLLA (cf. Nicotra, Babicka & Westoby 2002, Markesteijn & Poorter 2009), perhaps because these allow them to forage better for nutrients in more nutrients leached environments (cf Swaine 1996). Additionally, because of cheap construction cost a high SRL may be advantageous for carbon limited plants, growing in a low light environment. In a study of West African tree species Marhajan *et al.* (2011) found that high rainfall area species were evergreen and had denser wood, which may protect them against pathogens (Augspurger & Kelly 1984) and provide greater resistance against physical damage from falling debris (Van Gelder, Poorter & Sterck 2006). We found stem density and LAR being negatively correlated with R_{min} (cf. Poorter & Markesteijn 2008). Dry forest species (species with low R_{min} and also deciduous) had high LAR contrary to our predictions. This could be associated with less protection against herbivores in dry forests. Pest pressure increases with rainfall and wet forest species have long-lived leaves with low SLA, which protect them against herbivores and pathogens (Brenes-Arguedas *et al.* 2009).

Relationship between drought survival and species position along rainfall gradient

We hypothesised that (1) drought survival would be a good predictor of species position along the rainfall gradient, and (2) similar traits will determine drought survival and species distribution. The traits that best predicted drought survival (LMF, LDMC and RDMC) were not the same traits that best predicted species distribution (SLA), although all these traits were significant in both models. Surprisingly, we neither found a significant relationship between drought survival and species rainfall minimum. Our findings are in sharp contrast to findings of earlier studies (Engelbrecht *et al*. 2007, Poorter & Markesteijn 2008, Baltzer *et al*. 2008) that found a significant relationship between experimental drought survival and species distribution. Engelbrecht *et al*. (2007) found that species that were highly sensitive to drought occurred at the wet end of their climatic gradient. Baltzer *et al*. (2008) found that physiological drought tolerance was related to species distribution, with widespread species that occur in dry forest exhibiting physiological drought tolerance (ability to continue physiological function at low leaf water potential). It is possible that our experimental way of quantifying drought survival was not the right one. First, species were growing in a restricted volume of soil in pots, and could not forage in deeper soil layers for water, as they would do in a natural environment (Engelbrecht *et al*. 2005). Second, the results could have also been confounded by plant size, as large plants may deplete soil water more rapidly, because of their deep roots and large transpiring leaf area. However, this is not likely the case for our study; we included plant height as a covariate in our survival analysis, and it did not have a significant effect. Engelbrecht *et al.* (2005) neither found an effect of plant size on drought survival in the field. Field experiments are needed to clarify the relationship between drought survival in the field, and species position on the rainfall gradient. In a reciprocal transplanting experiment with the same species in the field, we found that the ratio of species survival in the dry forest relative to the wet forest correlated negatively with species position on the rainfall gradient (L. Amissah, unpublished data). This shows that species that survive relatively well under dry conditions occur in drier areas, and that drought performance plays an important role in shaping species distribution.

Our current results also suggest that species drought performance is not the only factor influencing species distribution patterns. Other factors such as herbivory (Brenes-Arguedas *et al*. 2009), light (Brenes-Arguedas *et al*. 2011), soil nutrients and geological substrate (John *et al.* 2007, Fayolle *et al.* 2012), history of forest formation (Jahn 1996), seed and dispersal limitation (Levine & Murrell 2003) and disturbance such as fire (Hawthorne 1994) shape species distribution along environmental gradients as well.

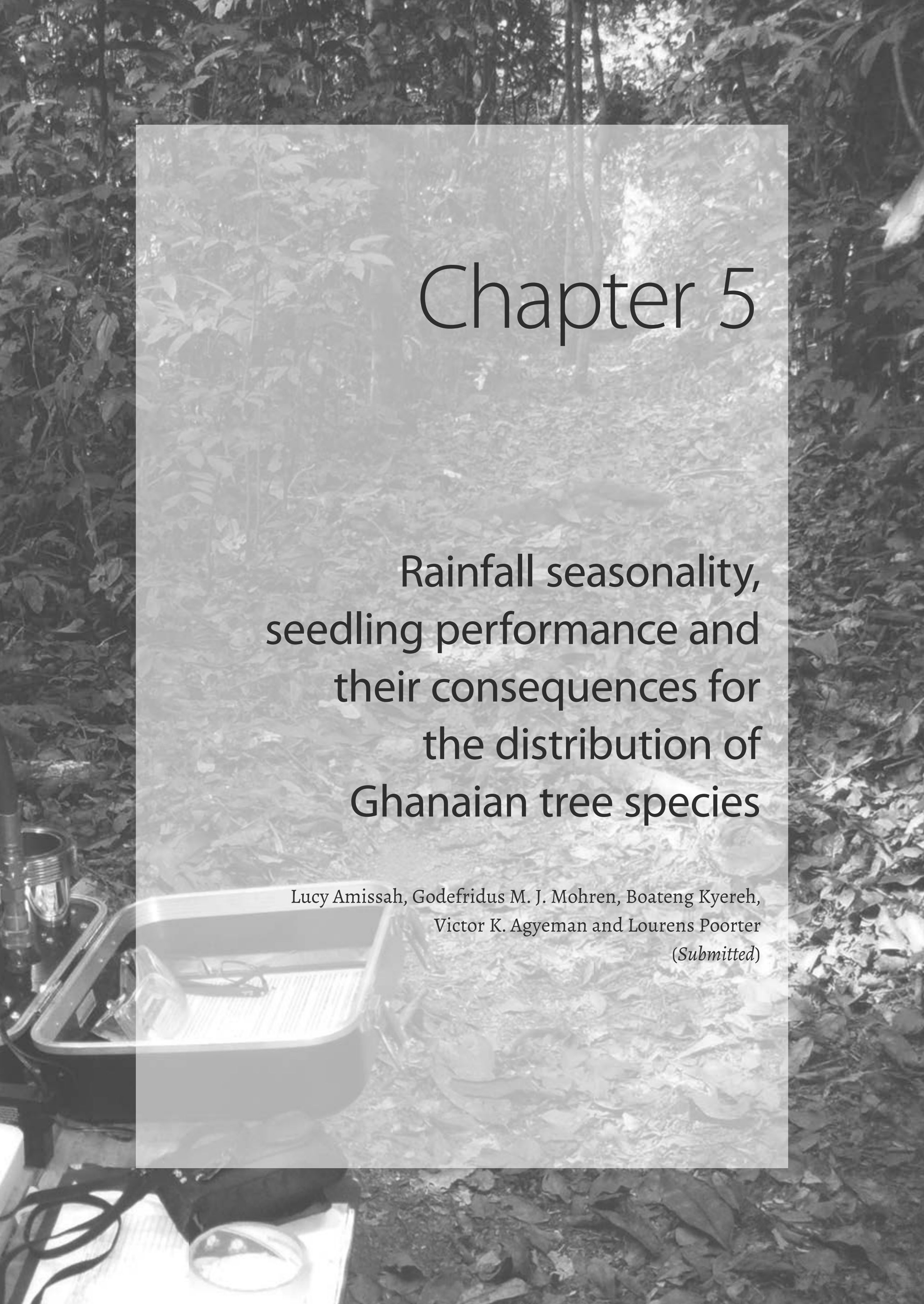
ACKNOWLEDGEMENTS

The authors thank Netherland Fellowship Programme (Nuffic), Wageningen University and the Council for Scientific and Industrial Research- Forestry Research Institute of Ghana (CSIR-FORIG) for providing funding for the study, and William Hagan–Brown, Elvis Nkrumah and Nana Prempeh Bandoh for assistance with data collection.

Appendix 1. Regression models fitted for traits of species growing under 5% full sunlight, drought survival after seven weeks and species annual rainfall minimum (R_{min}). The importance of traits and their coefficients (Beta) are shown. Significant traits are shown in bold based on 95% confidence interval. The R^2 for the fitted model for drought survival and traits is $r^2 = 0.03$, n = 24 and that for fitted model for species rainfall minimum is $R^2 = 0.10$, n =18. See text for traits abbreviation.

Traits	Drought survival		R_{min}	
	Importance	Beta	Importance	Beta
LMF	0.27	**-0.25**	0.20	**-0.25**
LDMC	0.32	**0.31**	0.17	-0.03
RDMC	0.20	**-0.12**	0.20	**-0.23**
RMF	0.23	0.07	0.25	**0.33**
SD	0.17	-0.00	0.17	**-0.15**
SLA	0.18	0.01	0.44	**-0.42**
SRL	0.25	**0.20**	0.18	**-0.19**
LWP_{ndDry}	0.29	**-0.27**	0.17	**0.18**
RLLA	0.36	**0.35**	0.18	**0.14**
LWP_{swDry}	0.17	0.12	0.29	**-0.33**


JOFFIL WAV



Chapter 5

Rainfall seasonality, seedling performance and their consequences for the distribution of Ghanaian tree species

Lucy Amissah, Godefridus M. J. Mohren, Boateng Kyereh,
Victor K. Agyeman and Lourens Poorter
(*Submitted*)

Abstract

Tree species distribution in lowland tropical forests is strongly associated with the annual amount and seasonality of rainfall. However, few studies have tested the performance of individuals of the same species in areas with contrasting rainfall amount and seasonality and even fewer studies have related species performance in the field to their position on the rainfall gradient. We carried out a reciprocal transplanting experiment in gaps in dry and wet forests in Ghana, using seedlings of 23 tree species that show contrasting rainfall distributions (dry, ubiquitous, and wet). We investigated seasonal patterns in environmental conditions, seedling performance (survival and growth) and leaf physiology over a 2-year period and related seedling performance to the species distribution along the rainfall gradient. Seasonal drought was longer in the dry forest (4 months) than in the wet forest (1.5 months) and was associated with higher vapour pressure deficit (2.0 vs. 0.6 kPa) and lower soil matric potential (-5.0 vs. -0.6 MPa) in the dry season. Seasonal drought led to a reduced leaf water potential and stomatal conductance in all species, but dry forest species had lower leaf water potentials and higher conductance than wet and ubiquitous species, indicating a higher physiological capacity to tolerate drought stress. Seasonal drought led to a significant reduction in survival and growth in the wet species in the dry forest compared to ubiquitous species and dry forest species. Dry forest species showed a home advantage, and realized higher survival and growth than wet forest species, not only in the dry forest but also in the wet forest. The ratio of species survival in the dry forest relative to the species survival in the wet forest correlated negatively with species position on the rainfall gradient, and the same applies for the ratio of the height growth rates. This indicates that species that survive and grow relatively well under dry conditions occur in drier areas, and that drought performance plays an important role in shaping species distribution. Many climate change models predict an increase in frequency of drought, and our results suggest that this is likely to cause a shift in the distribution of species that occur at the wetter end of the rainfall gradient.

Key Words: Drought survival, dry forest, growth, stomatal conductance, leaf water potential, wet forest, rainfall.

INTRODUCTION

Forest diversity, structure, composition and distribution vary markedly along the rainfall gradient (Hall & Swaine 1976, Gentry 1988, Bongers *et al.* 1999, Davidar *et al.* 2005). A complex of other factors (e.g. understory light, soil and herbivory) may co-vary along the rainfall gradient and affect the performance of individual species and ultimately their distribution (Swaine 1996, Brenes-Arguedas *et al.* 2009). To get insight into what is really affecting species performance and distribution requires the monitoring of environmental conditions as well as assessing seedling performance in a reciprocal planting experiment in contrasting forest sites. Among the environmental factors affecting species distribution, seasonality of rainfall has been found to be one of the best correlates of the distribution of individual species (Condit 1998, Veenendaal and Swaine, 1998, Bongers *et al.* 1999, Condit *et al.* 2013). Seedlings are likely to be most sensitive to seasonal drought (Mulkey *et al.* 1991, Gerhardt 1996, Marod *et al.* 2002,) because of their small size and shallow root system which impede adequate access to deeper soil layers to forage for water (Poorter & Hayashida-Oliver 2000, Tyree *et al.* 2003). Even in very wet aseasonal tropical forests, short dry spells have been shown to cause stress and mortality in pioneer seedlings (Engelbrecht *et al.* 2006). It is expected that seedling drought performance explains species distribution (cf Engelbrecht *et al.* 2007, Baltzer *et al.* 2008) and consequently dry forest species should survive and grow better in dry forest than wet forest species and vice versa. Increased drought mortality may explain why wet forest species are excluded from dry forest, where there is a longer and more intense dry season. However, it does not explain why dry forest species are excluded from wet forests. Perhaps dry forest species possess physiological adaptations to perform better at low water availability (Hacke *et al.* 2006) and hence should be at a disadvantage when growing in an area with high water availability (Baltzer & Davies 2012). In contrast wet forest species may possess little or no adaptation for tolerating low water availability and therefore should be at a disadvantage in dry forests (Kursar *et al.* 2009).

Seasonality in irradiance occurs throughout the tropics (Wright & van Schaik 1994) and influences seasonal variation in net primary production both in evergreen and deciduous forests (Raich *et al.* 1991). Photosynthetically active radiation (PAR) is very important for plant growth because it is directly related to photosynthesis (Tserenpurev *et al.* 2012). PAR increases during the dry season when it is less cloudy and most leaves are shed (especially in the dry forest) and decrease in the rainy season after leaf flushing (Wright & Cornejo 1991). In dry forest the canopy is more open and sparse during the wet season and contains a higher percentage of deciduous species during the dry season. Consequently, PAR is expected to be much higher in dry than in wet forest. An increase in irradiance is associated with an increase in temperature and decrease in relative humidity, leading to a high vapour pressure deficit and increased evaporative demand on plants. As a result, evapotranspiration has been found to be generally higher in the dry season than in the wet season (Costa *et al.* 2010).

Soil fertility has been identified as one of the key factors that could also explain the distribution of tropical species, and importantly, can explain the exclusion of dry species from wet forests. Wet forest soils are generally low in pH and in base saturation and cation exchange capacity than dry forest soils, due to more leaching in wet forest soils (Murphy & Lugo 1986, Veenendaal & Swaine 1998). Consequently, species that are intolerant to low nutrients are not likely to perform well in wet forest. However, in controlled greenhouse experiments in Ghana only few species were found to show significant growth responses to soil fertility (Veneendaal *et al.* 1996c, Amissah *et al.* unpublished data), and transplanting experiment in the field neither gave evidence for a soil home-advantage to species (Swaine *et al.* 1997).

Pest pressure may co-shape species distribution along the rainfall gradient, as herbivore damage may aggravate the effects of drought and limit species distribution (Baltzer & Davies 2012). The general hypothesis is that herbivore pressure is greater in wet tropical forests than in dry tropical forests (Connell 1971, Coley & Barone 1996). Dry forest species may have evolved therefore less defence mechanism against pests (Coley & Barone 1996) which could decrease their performance when growing in a wet forest where they might suffer from high herbivory rates (Baltzer & Davies 2012). Wet forest species should also experience less damage in dry forest because they possess better defence mechanism than dry forest species. However, recent studies (Brenes-Arguedas *et al.* 2009, Baltzer & Davies 2012) have found no evidence for such distribution-based differences in vulnerability to herbivores.

Water availability has a large effect on primary production of about 40% of vegetated land (Beer *et al.* 2010). It strongly shapes the physiology and hence growth and survival of plants. In a study in an Indian tropical dry forest stomatal conductance explained 62% of variability in RGR across spatial and temporal gradient of soil water availability (Chaturvedi *et al.* 2012). At soil matric potential below -1.5 MPa plants reach their permanent wilting point (Gerhardt, 1993). Plants in moist tropical forest can be exposed to considerable drought stress during the dry season with leaf water potentials being as low as -3.5 MPa (Becker & Wong 1993, Condit *et al*. 1995, Veenendaal *et al*. 1996a, Tobin *et al*. 1999) whereas soils are nearly saturated during the wet season (Comita & Engelbrecht 2009) and even in dry forests leaf potential can be above -0.5 MPa in the wet season (Choat *et al*. 2006). As a result, most tropical tree species reduce their physiological activity in the dry season, and species vary in their adaptive capacity to regulate for example leaf photosynthesis between seasons (Craven *et al*. 2011).

Few studies (but see Swaine *et al*. 1997, Brenes Arguedas et *al*. 2009, Baltzer & Davies 2012) have used reciprocal transplanting experiments to assess survival, growth and physiological tolerance of seedlings to drought stress. Such studies can help to confirm results of greenhouse experiment and also enhance our understanding of how individuals of the same species perform in- and acclimate to- different forest environments. Here we present a reciprocal transplanting experiment in Ghana, where we planted seedlings of 23 species with contrasting distribution along the rainfall gradient (dry, ubiquitous, moist and wet) in gaps in a wet forest and a dry forest. We investigated seasonal patterns of environmental factors and monitored seedling performance (survival and growth) and physiology for a 2-year period. We addressed three questions and their corresponding hypotheses: (1) How do environmental conditions (e.g. soil matric potential, irradiance, vapour pressure deficit) vary between dry and wet forests? We hypothesised that the dry season will be longer in dry forest with a higher temperature and lower relative humidity in the dry season compared to the wet forest. Irradiance at the gap floor will be higher in the dry forest than wet forest, and this will even be more pronounced in the dry season when most dry forest canopy trees shed their leaves. (2) How do seedlings of different species perform in terms of growth, survival and physiology in dry and wet forests? We hypothesised that (a) Seedlings growing in dry forest will have a lower leaf water potential during the dry season than those in the wet forest. Dry-distributed species will sustain higher stomatal conductance despite a lower leaf water potential than wet-distribution species in dry forest, and b) species will have a home advantage, and wet-distribution species will perform (survival and growth) better than dry–distribution species in wet forest and vice versa and (3) Does drought survival and growth in the field determine species distribution along the rainfall gradient? We hypothesised that the ratio of drought survival and growth in the dry forest relative to the wet forest will correlate negatively with species position on the rainfall gradient. That is, species that exhibit low drought survival and growth in the dry forest relative to the wet forest will occur at the wetter part of the rainfall gradient (Engelbrecht *et al*. 2007).

MATERIALS AND METHODS

Study sites

The study was conducted in two forest reserves with contrasting characteristics; the Afram Headwaters Forest Reserve (Fig.1a), which is a dry forest and Neung South Forest Reserve (Fig. 1b), which is a wet forest. Afram Headwaters Forest Reserve is classified as a dry semi-deciduous forest inner zone subtype (Hall & Swaine 1981). It covers an area of 201 km^2 and lies on longitude 1° 32' W and 1° 48' W and latitude 6° 45 'N and 7° 25' N. The altitude varies from 274- 412 m above sea level. There are few steep slopes in the eastern part. The area in general is a plateau with numerous streams draining it. The reserve is characterized by uniform high temperatures and two peak rainfall seasons in June and October and a dry season from November to March. There are two well defined rainfall peaks, the higher in June and the lesser in October. Mean annual rainfall, mean maximum temperature and mean minimum temperatures are 1243 mm ± 63, 30.6 ± 0.24°C and 21.2 ± 0.23°C, respectively. The soil varies from reddish to reddish brown in colour. Over most of the area the soil is sandy loam with patches of clay (Forestry Division 1963). The Neung South Forest Reserve is classified as wet evergreen forest (Hall & Swaine 1981). It is located between longitude 1° 55' W and 2° 07' W and latitude 05°06' N and 5° 11' N. The reserve has an area of 113 km^2 of which 73 km^2 is designated as Globally Significant Biodiversity Area (GSBA) because of its relatively high plant species diversity. The reserve comprised of a range of small hills and ridges with an average altitude of about 150 m above sea level. The area lies within the Equatorial Climatic Zone which is characterised by double maxima rainfall starting from March to September. Average annual rainfall is 1880 mm. Temperatures are fairly uniform and range between 26°C (in August) and 30°C (in March). Relative humidity is generally high throughout the year; 70% – 80% in the dry season and 75% – 80% in the wet season. The soil texture in most parts of the reserve is loamy-clay (Forestry Commission 2007).

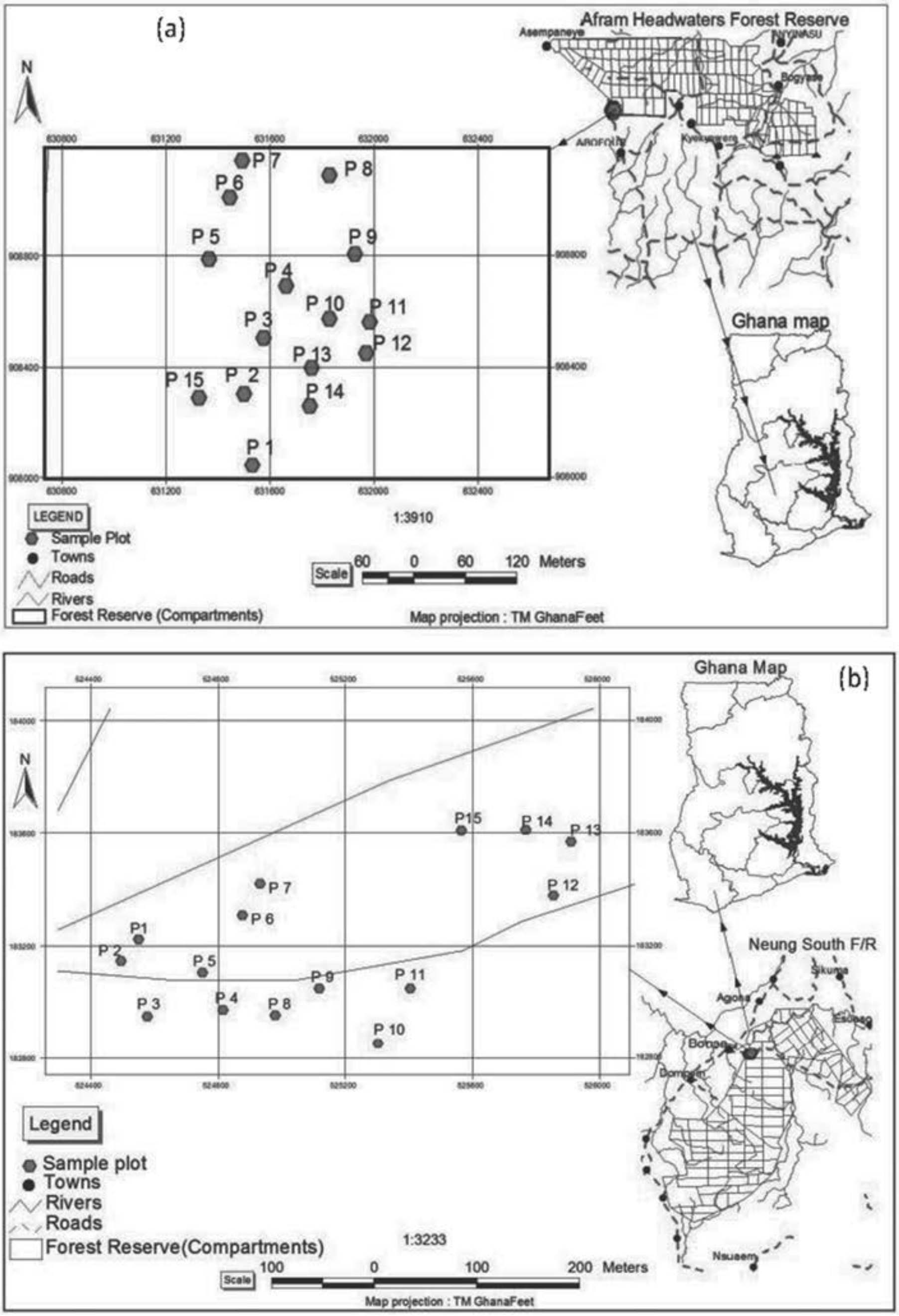


Figure 1. Map showing the distribution of plots in the two forests used for the reciprocal planting of 23 species and their location in Ghana. (a) dry forest and (b) wet forest.

Species selection and experimental design.

Twenty three species were selected based on four criteria: (1) importance as timber and medicinal plant, (2) natural distribution, (3) light requirement for regeneration and (4) availability and germination of sufficient seeds (Appendix 1). Species were assigned to three distribution types; dry forest species (10 species), mix of moist and wet forest species (8 species), hereafter refer to as “wet” species and ubiquitous species (5 species). Twelve of the species are non-pioneer light demanders, 8 are pioneers and 3 are shade tolerant. Seeds of the 23 species (Appendix 1) were collected from the dry forest (Afram Headwaters Forest Reserve), moist forest (Bobiri and Pra-Anum Forest Reserves) and wet forest (Neung South and Subri Forest Reserve) from November 2010 - March 2011, from 4-5 seed trees per species. Most (70%, 7 of 10 species) of the dry forest species seeds were collected from Afram Headwaters and 88% (7 out of 8 species) of the wet species were collected from wet forest (Neung South) and moist forest (Bobiri Forest Reserve). For the ubiquitous species 2 were collected from Afram Headwaters Forest Reserve and 2 from Bobiri Forest Reserve. In the case of the ubiquitous *Terminalia ivorensis*, there were two genotypes from wet and dry forests. Seeds were germinated in germination bowls and after 2-3 weeks seedlings were transplanted to individual polybags that were 12.7 cm wide and 20.3 cm long. Polybags were filled with soil collected from moist semi-deciduous forest (Bobiri Forest Reserve). The seedlings were grown for 2-4 months (except for *Turraeanthus africanus, Lophira alata, Strombosia pustulata* and *Nesogordonia papaverifera* that were between 10-12 months; seedling were grown in large poly bags of 19 cm wide and 46 cm long) in a shade house of ca.15% full irradiance before being planted in the field. The 15% irradiance enhances maximum growth of seedling at the nursery stage (Agyeman *et al.* 1999). Seedlings were watered daily in the mornings during the period they grew in the shade house. For the transplanting experiment, fifteen naturally occurring gaps were selected for each site (Fig. 1a & b). To obtain on average 20% irradiance for each plot additional trees were felled from the selected gaps. Plot sizes for the planting trial were 9 m x 8 m for 13 plots per site and 12 m x 6 m for 2 plots in each site. These plot sizes were the sizes used for the planting trial but the gap border started at ca. 2 m from the trial edge. Irradiance measurements were conducted in each gap over a period of 2-4 weeks with a Fisher Scientific Traceable Dual Display light meter (Fisher Scientific Company, IL, USA). The slope of each plot was measured for all the plots using a clinometer (Clino Master - Sisteco Precision, Finland). Average slope of plots in the dry forest was 10.1% (std. = 3.1) and in the wet forest was 12.7% (std. = 4.7). Plots were on average 72 m (std. = 47) apart in the wet forest and 74 m (std. = 34) apart in the dry forest. Plots were oriented east-west to ensure that the diurnal course of the sun had a similar effect on all gaps. Seedlings were planted at a planting distance of 1 m in a complete randomized design with 4 replicates per species. The only exception was *Tieghemella heckelii* which had one individual per species in each plot. To minimise planting damage, seedlings were planted with the soil that was in the plant bag, after removing the bag. Individual seedlings were planted in June 2011, first in the dry forest and a week later in the wet forest. A total of 2670 seedlings were planted: (2 forests x 15 gaps x 22 species x 4 individuals per species) + (2 forests x 15 gaps x 1 species x 1 individual per species). Average seedling size of species was 24.5 cm tall at planting (range 8.5-63.4 cm). Plots were weeded three times in a year. Survival of species was assessed two months after planting and dead seedlings were replaced.

Environmental data

To monitor monthly rainfall a manual rainfall gauge was installed about 3 km from each forest in June 2011. To monitor relative humidity and temperature in the plots, in January 2012 (six months after planting) in each forest, HOBO Prov2 temperature/relative humidity data loggers (Onset Computer Corporation, USA) were installed in two plots (plots 1 and 10 in the wet forest, and plot 3 and 7 in the dry forest) and outside in an open area about 1 km from the forest. PAR was measured in each plot in two dry seasons and one wet season. PAR was measured with LI-190SA Quantum Sensor (LI-COR INC., Lincoln, Nebraska, USA) placed both outside (under full sunlight) and inside the plots. At each census, irradiance was also measured in all 15 plots at each site. To this end, the sensors were moved from one plot to the other until all 15 plots were characterised. Measurements were conducted in the morning and in the afternoon for all 15 plots in 2-3 consecutive days. In the plots, LI- 1400 data logger (LI- COR INC., Lincoln, Nebraska, USA) and the quantum sensor were placed at the centre of the plots for 10 minutes. Average PAR was logged at a sampling period of 5 minutes (i.e. two average PAR readings were logged in 10 minutes). A LI-1000 data logger (LI-COR INC., Lincoln, Nebraska, USA) was used to take instantaneous PAR readings outside the plots under full sunlight. Simultaneous readings of temperature and relative humidity were made alongside PAR measurement. Simultaneous readings of temperature and relative humidity (RH) in the plots were used to calculate vapour pressure deficit (VPD) in the plots. An existing look-up table was used to ascertain the saturated vapour pressure (SVP) for a given temperature and then VPD was calculated as: VPD = ((100 - RH)/100)*SVP.

To quantify soil water availability, soil samples were taken for 11 plots per forest for two dry seasons (January 2012 and January 2013) and a wet season (July 2012). In each plot, soil samples were taken at five positions (four corners and the centre of the plot) and five depths (10 cm, 20 cm, 30 cm, 40 cm, and 60 cm), providing a total of 1,650 soil samples (2 sites x 11 plots x 5 positions x 5 depths x 3 time periods). Soil matric potential was estimated using the filter paper technique (Deka *et al.* 1995). Plastic containers were half-filled with collected soil samples and covered with three filter papers (Whitman 42, 55 mm , batch nos. 5365518 and 9118643) (GE Healthcare, Limited, UK) and topped with another half of the soil sample. The soil was firmly pressed to prevent air pockets from forming and hermetically sealed with black tape (PVC tape for electrical insulation, 0.13 mm x 19 mm, Detat Industries Corporation, China). The soil was incubated for 7-14 days. After the incubation period filter papers were carefully removed, weighed and dried at 105°C for 24 hours and reweighed. With the dry mass of the filter paper known, the moisture content of filter paper (FMC) was used to estimate soil matric potential in line with the protocol described by Deka *et al.* 1995 in which;

$\mathrm{Log}_{10}(-\Psi p) = 5.144-6.699 * \mathrm{FMC}$, if $\Psi p <- 51.6 \mathrm{KPa}$

$\mathrm{Log}_{10}(-\Psi p) = 2.383- 1.309 * \mathrm{FMC}$, if $\Psi p >- 51.6 \mathrm{KPa}$

To quantify soil fertility for each site, soil samples were taken from the upper 20 cm in February 2013. In each forest, 5 samples were taken per plot for all 15 plots. Samples were stored in sealed plastic bags and transported to the laboratory where they were air-dried, and then packed in sealed plastic bags. To characterise the fertility level of each forest a bulk sample was made from the samples from all plots in each forest (i.e. equal amount of soil was taken from each plot sample and mixed together). Soil pH and nutrient (base saturation, cation exchange capacity, available P, K, nitrogen and carbon) analyses were carried out at the laboratory of the CSIR-Soil Research Institute of Ghana.

Seedling performance and leaf physiology measurements

Height, diameter and leaf number (for compound leaves, we counted the leaves and not leaflet) were measured for each seedling every two months throughout the 24 months period, except between the last two measurements where the interval was four months. During each census survival and mortality were assessed. Seedlings were considered to be dead if the stems were brown and there was necrosis on all leaves, extensive leaf curling, and brittle leaf blades (cf. Gerhardt 1993, Tyree *et al.* 2002). At the next census seedlings that were recorded dead were rechecked; if a species had resprouted after being recorded as dead, data were corrected. Height was measured as the vertical distance between the forest floor and the apex. Stem diameter was measured at 10 cm height from ground level.

Leaf physiology (leaf water potential and stomatal conductance) was measured for the two dry seasons (2012 and 2013) and one wet season of 2012 in 11 plots per forest. For the wet season, stomatal conductance was measured in fewer plots (5 plots per sites) because cloudiness of the weather made measurements difficult (as RH was too high leading to hysteresis). For stomatal conductance measurement two individual per species per plots were sampled. For the first individual also a leaf sample was taken to determine the leaf water potential. In total ca. 2,484 leaf conductance measurements were made (2 forests x 2 dry seasons x 11 plots x 23 species x 2 seedling per species + 2 forests x 1 wet season x 5 plots x 23 species x 2 seedlings) and 1,242 leaf water potential measurements. Leaf water potential and stomatal conductance were measured on a fully-matured leaf without damage at about the third position from the apex. Leaf water potential was measured using the pressure bomb technique (Tyree & Hammel 1972, SKPM 1405/80, Skye Instruments Ltd, UK). Leaf water potential was measured at both pre-dawn (from 5:30-8:30 am), and around mid-day (from 11:30 am to 2:00 pm). Stomatal conductance was measured throughout the day from 8:30 am to 3 pm, but for each seedling at a single moment in time. When the morning was cloudy measurement started at 10:00 or 11:00 am. Stomatal conductance was measured with a leaf porometer (Model SC-1, Decagon Devices, Inc. USA) on attached leaves. Measurements were made at the abaxial surface (Wright and Cornejo 1990) because that is where most stomata are located. The measurements of leaf water potential and stomatal conductance were made on the same individuals for the two dry seasons and the wet season. However, when an individual died it was replaced with another individual during the measurement.

Data analysis

For each seedling absolute growth rate (AGR) in height, diameter, and leaf number were calculated as the difference in growth between the last census (at 2 years) and the first census at planting divided by the time difference between the two censuses. Relative growth rate (RGR) was calculated as the difference between the natural ln transformed values for individuals at the last census (2 years) and at planting divided by the difference between time at the beginning and end of the censuses. One of the hypotheses is that species have a home advantage, and species distribution type (dry, ubiquitous, wet-moist) was therefore included as a factor in many analyses. Repeated measures ANOVAs were used to analyse the effects of forest type and season on environmental variables (PAR, temperature, relative humidity, VPD, soil matric potential) and leaf physiology (leaf water potential and stomatal conductance). A mixed ANOVA was used to test the effects of forest type, seasons and species distribution type on absolute growth and relative growth rate of height, diameter and leaf number, including plots as random factor. To assess the physiological performance of species with contrasting distribution in each forest the repeated measures ANOVA was carried out separately for each forest site. Values of absolute growth in height, diameter, leaf number, and stomatal conductance were $\log_{10}$ transformed to achieve normality and stabilise the variance. Leaf water potential and soil matric potential were also log transformed ($-\mathrm{Log}\ (-\Psi\ +1)$). A survival analysis could not be conducted using the normal Kaplan–Meier procedure because most of the species in both the dry and wet forests had more than 50% survival at the end of the experiment. Percent survival was therefore calculated as the number surviving at the end of two years relative to survival two months after planting in the field. The effect of forest type and species distribution type on survival (in percentage) was tested with a two-way ANOVA. Effect sizes of individual factors were calculated as the sum of square of the effect divided by the total sum of square of all effects in the model and their errors terms excluding the sum of square for the intercept. For the repeated measure ANOVAs effect sizes were calculated separately for the within subjects effects and between subject effects, hence total effects size for the between subject and within subject effects will be greater than 100%. Relative performance in the field was quantified in terms of survival as the ratio of percent survival in the dry forest relative to wet forest (Engelbrecht & Kursar 2003). Relative growth performance was quantified similarly as the ratio of absolute growth rate in the dry forest over absolute growth rate in the wet forest. To evaluate whether species performance (survival and growth) in the field is a good indicator of species position on the rainfall gradient, a Spearman's rank correlation was conducted between relative field performance and species rainfall minimum and optimum as determined from individual species response curves (see Amissah *et al.* in press).

RESULTS

Variation in environmental conditions between dry and wet forest

Mean amount of rainfall did not differ significantly between the dry and wet forests over the two-year experimental period (T test, t = 1.753, P = 0.086, df = 46, n = 24). However, there was a longer dry season in the dry forest than in the wet forest (Fig. 2a, b). In 2012, the length of the dry season (defined as months with less than 100 mm rain) was 5 months in the dry forest (Fig. 2a), and 2 months in the wet forest (Fig. 2b). In 2013, the length of the dry season was 3 months in the dry forest and 1 month in the wet forest (a short dry period in February; Fig. 2b). Total rainfall during the 2 years experiment was 3439 mm in the wet forest and 2174 mm in the dry forests. The other environmental conditions varied significantly between forest type and seasons (Table 1, Fig. 3). Most of the variation was explained by forest type (with an average effect size of 70.9%), followed by season (average effect size of 63.5%), and their interaction (average effect size of 19.8%). PAR varied significantly between dry and wet forests as well as between the dry and wet seasons but there was no significant interaction between forest type and season (Table 1), which is an indication that both forests showed a similar seasonal variation. PAR was higher in the dry season than in the wet season in both forest types and also higher in the dry forest than in the wet forest (Table 1, Fig. 3a). Temperature and relative humidity varied significantly between forest types and also between seasons with a significant interaction between forest type and season (Table1). For both forest types, temperature was higher in the dry season than in the wet season (Fig. 3b). However, in the wet season temperature was higher in the wet forest than in the dry forest (Fig. 3b). Relative humidity was lower in the dry forest than in the wet forest and was also lower in the dry season than in the wet season in both forest types (Fig. 3c). Vapour pressure deficit differed significantly between dry and wet forests, and between the dry and wet seasons with a significant interaction between forest type and season (Table 1). This indicates that dry and wet forests showed different seasonal variation in VPD. VDP was higher in the dry forest than in the wet and also higher in the dry season than in the wet season forest (Fig. 3d).

Soil from the wet forest was more acidic and lower in N, C, available P and K, base saturation and exchangeable cations (Ca, Mg, K and Na) than soil from the dry forest (Appendix 2). This indicates that soils from the wet forest are less fertile.

Table 1. Seasonal variation in photosynthetically active radiation (PAR), temperature, relative humidity and vapour pressure deficit (VPD) between dry and wet forests. The table shows the results of ANOVA with season as repeated measure, forest type (FT) as independent variable and PAR, temperature relative humidity and vapour pressure deficit as dependent variables. F values for within and between subjects effects are given. Significance of F values are given as $^{**}P \leq 0.01$; $^{***}P \leq 0.001$. n = 15 for all three dependent variables for each forest type. Effect size (η^2) for each independent variable is given in parentheses.

Variable	Forest type (FT)	Seasons (S)	S x FT
PAR	49.9*** (64.0%)	18.9*** (38.9%)	1.6 (3.4%)
Temperature	9.4** (25.1%)	260.6*** (65.5%)	109.0*** (27.4%)
Relative Humidity	2023.4*** (98.6%)	5567.8*** (76.3%)	1700.1*** (23.3%)
VPD	664.4*** (70.9%)	1485.2*** (73.8%)	497.9*** (24.7%)

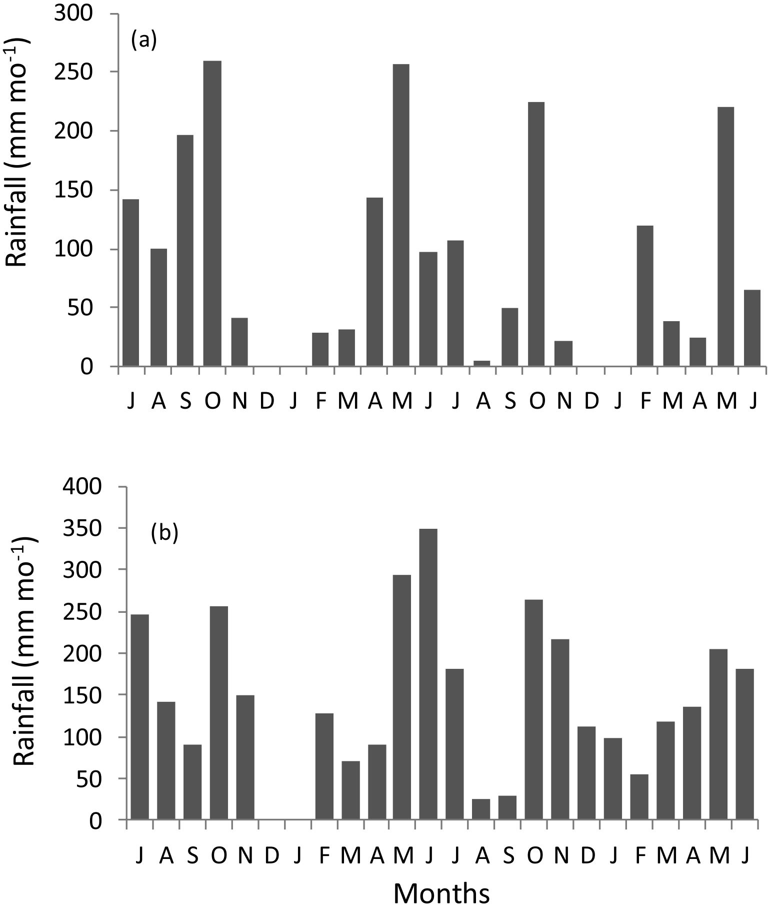


Figure 2. Seasonal variation in monthly rainfall from July 2011-June 2013 in (a) dry forest and (b) wet forest. Monthly rainfall was compiled from daily rainfall collected from a manual rainfall gauge placed about 3 km from each forest.

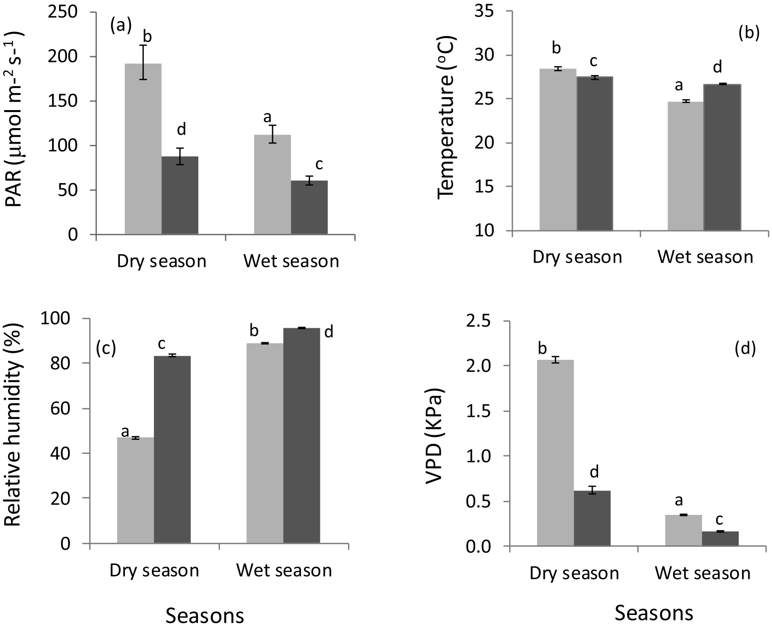


Figure 3. Variation in environmental variables in dry and wet seasons between dry forest (grey bars) and wet forest (black bars): (a) Photosynthetically active radiation (PAR), (b) Temperature, (c) Relative humidity and (d) Vapour pressure deficit (VPD). Means and standard errors are shown. Bars accompanied by different letter are significantly different at $P < 0.05$ (Bonferroni Post-Hoc test).

Seasonal variation in soil water availability

Soil matric potential (Ψ_{soil}) varied significantly between dry and wet forests and between seasons, and with soil depth (Table 2, Fig. 4). There was significant interaction between forest type and season (Table 2). Most of the variation in Ψ_{soil} was explained by forest type (81.3%), followed by seasons (69.9%), and the interaction between forest type and season (24.1%). The Ψ_{soil} was lower (i.e., more negative) in the dry forest than in the wet forest for all soil depths during the dry season (Fig. 4a, b). Ψ_{soil} increased (i.e., became less negative) with depth in the dry forest during the dry season from 10 cm to 20 cm depth. Ψ_{soil} at 30 cm and 40 cm depth was not significantly different from 20 cm depth. Ψ_{soil} of soil depth 60 cm was significantly different from all soil depth (Fig. 4). The topsoil (0-10 cm) was the driest and was significantly different from soils of all other depths (20 cm, 30 cm, 40 cm, 60 cm) in the dry forest during the dry season (Bonferroni post hoc test, $P < 0.001$). In the dry season the top 0-10 cm, was -5.02 MPa at the dry forest and -0.64 MPa at the wet forest (Fig. 4b). Bonferroni post-hoc tests showed that, in the wet forest, Ψ_{soil} at 10 cm depth was not significantly different from all the other depths in both dry and wet seasons. On average, in the dry season Ψ_{soil} was lower (-3.03 MPa) in the dry forest than in the wet forest (-0.43 MPa) across all soil depths. On average, in the wet season Ψ_{soil} was -0.04 MPa in the dry forest and -0.01 MPa in the wet forest across all soil depths.

Table 2. Seasonal variation in soil matric potential (Ψ_{soil}) between dry and wet forests. The table shows the results of ANOVA with season as repeated measure, forest and soil depth as independent variable and Ψ_{soil} as dependent variable. F values for within and between subjects effects are given. Significance of F values are given as $^{***}P \leq 0.001$. n = 55 for each forest type. Effect size (η^2, in %) for each independent variable is given in parentheses.

Variable	Forest type (FT)	Seasons (S)	Soil Depth (SD)	FT x SD	S x FT	S x SD	S x FT x SD
Ψ_{soil}	978.1^{***} (81.3)	2968.4^{***} (69.9)	23.7^{***} (7.8)	7.4^{***} (2.4)	1022.4^{***} (24.1)	30.3^{***} (2.9)	8.2^{***} (0.7)

Seedling growth and survival in dry and wet forests

Seedling survival at the end of 24 months was significantly higher in wet compared to dry forest, but there was no significant effect of species distribution, and neither a significant species distribution x forest type interaction (Table 3, Fig. 5d). Absolute growth in height (AGR_{height}) varied significantly with forest type, species distribution, and their interaction (Table 3). AGR_{height} was, on average, higher in the wet forest compared to the dry forest (Fig. 5a). In the dry forests ubiquitous species had the highest $AGR_{height,}$ followed by dry species and wet species. In the wet forest, dry and ubiquitous species had significantly (all $P < 0.001$) higher AGR_{height} than wet species (Fig. 5a). Absolute growth in diameter did not differ significantly between forests but varied significantly with species distributions type, and the interaction between distribution type and forest type (Table 4). In the dry forests, dry species and ubiquitous species had significantly higher growth rates than wet species and in the wet forest dry species had significantly higher growth rates than the other two distribution groups (Fig. 5b). Absolute growth in leaf number followed the same pattern as absolute growth in diameter (Table 3, Fig. 5c). Patterns in absolute growth and RGR were very similar for the different growth variables, with the exception of RGR_{leaves} for which there was a forest type effect (Table 3). Therefore we only present here the absolute growth values. For the RGR values, see Appendix 3.

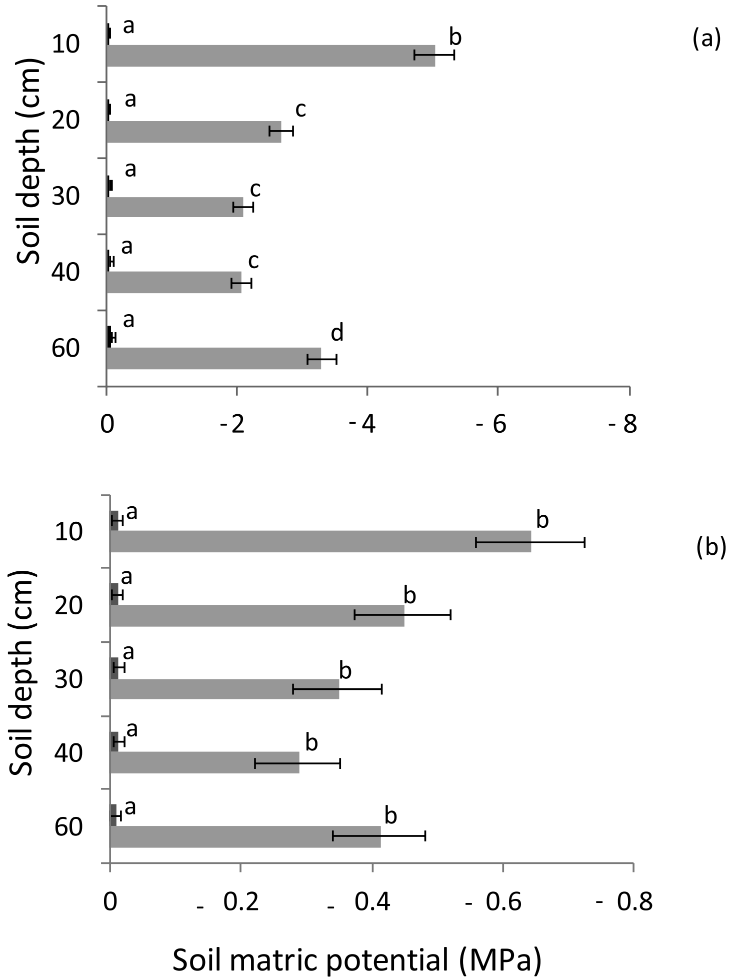


Figure 4. Dry season (grey bars) and wet season (black bars) variation in soil matric potential in (a) dry forest and (b) wet forest. Means and standard errors are shown. Bars accompanied by different letters are significantly different at $P < 0.05$ (Bonferroni Post Hoc test). Please note that the scaling of the x-axis differs between the two panels.

Table 3. Seasonal variation in absolute and relative growth rates (AGR and RGR) and survival of species with different distribution between dry and wet forests. The table shows the results of ANOVA with forest type (FT) and species distribution type (SPD; dry, ubiquitous, and moist/wet) as independent variable, plot as random factor and absolute growth and relative growth rates (RGR) in height, diameter and leaf number as dependent variables. F values and their significance are given. Significance of F values are given as $^{*}P \leq 0.01$; $^{**}P \leq 0.01$; $^{***}P \leq 0.001$.

Variable	Forest type (FT)	Species distribution (SPD)	Plot	FT x SPD
AGR_{height}	6.6^{*}	69.8^{***}	0.8	17.1^{***}
$AGR_{diameter}$	2.7	52.3^{***}	0.6	12.3^{*}
$AGR_{leafnumber}$	4.0	202.8^{***}	0.7	8.5^{**}
RGR_{height}	14.5^{**}	45.2^{***}	1.1	21.9^{***}
$RGR_{diameter}$	1.0	69.1^{***}	0.6	17.3^{***}
$RGR_{leaf\ number}$	8.1^{*}	182.9^{***}	0.9	4.9^{*}
$Survival_{24mths}$	5.0^{*}	1.7	NA	1.8

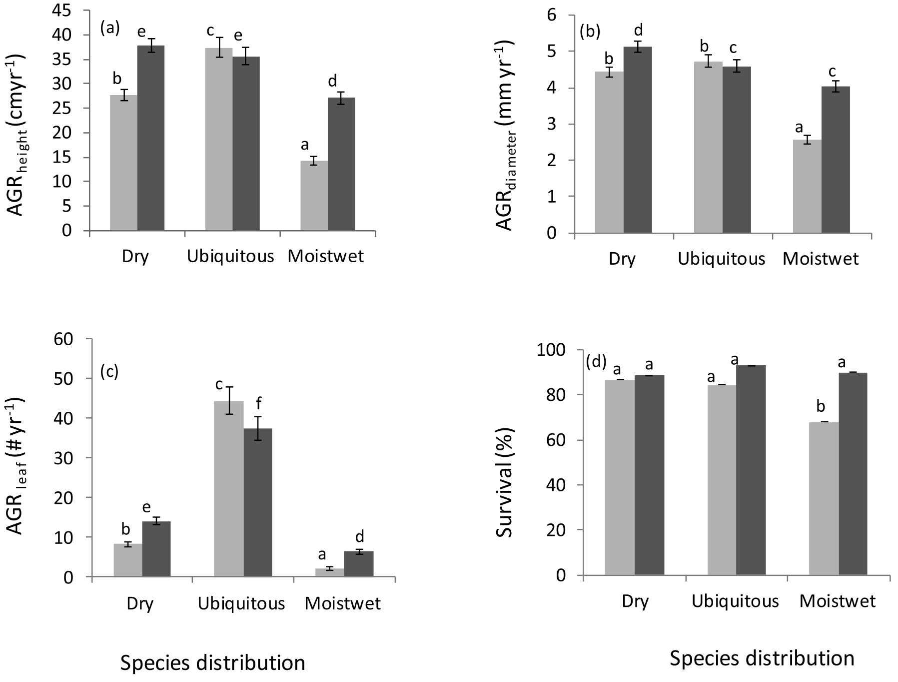


Figure 5. Absolute growth rate (AGR) and survival of species with different distributions (dry forest species, ubiquitous species and moist-wet forest species) in dry (grey bars) and wet (black bars) tropical forests at the end of 2-year period. (a) height growth (b) diameter growth (c) number of leaves, and (d) survival. Mean and standard errors are shown. Bars accompanied by different letters are significantly different at $P < 0.05$ (Bonferroni Post-Hoc test).

Effects of seasonal variation on leaf physiology

Across the three physiological variables (predawn and mid-day leaf water potential and stomatal conductance) evaluated, a similarly large variation was on average explained by season (32%), the season and forest type interaction (31.7%), and forest type (31.6%), followed by species distribution (7.8%). Mid-day leaf water potential (Ψ_{mid}) varied significantly with forest type, seasons and species distribution. There was a significant interaction between seasons and forest type but no interaction between forest type and species distribution (Table 4). In general, Ψ_{mid} was significantly lower in the dry season than in the wet season, and lower in the dry forest than in the wet forest (Fig. 6a). In both forest types, dry forest species had a significantly more negative Ψ_{mid} than the ubiquitous species and wet species across dry and wet seasons. Pre-dawn leaf water potential (Ψ_{pd}) followed a similar pattern as the mid-day leaf water potential (Ψ_{md}) (see Appendix 4). Stomatal conductance (g_s) varied significantly with forest type and species distribution, but not with season, although the interaction between season and forest type was significant (Table 4.) There was no significant interaction between species distribution and forest type, indicating the variation in stomatal conductance was similar in both forest types. There was an interaction between season and species distribution type which shows that species differ in their responses to seasons. Forest type explained the greatest variation in stomatal conductance (49.5%) followed by interaction between season and forest type (48.7%) and species distribution (5.3%). In general, stomatal conductance was higher in the wet forest than in the dry forest. In both seasons dry and ubiquitous species had significantly higher conductance than the wet species in the wet forest (Fig. 6b).

Table 4. Seasonal variation in pre-dawn (Ψ_{pd}), mid-day leaf water potential (Ψ_{mid}) and stomatal conductance between dry and wet forests. The table shows the results of ANOVA with season as repeated measure, forest type and species distribution (dry, ubiquitous, and moist/wet) as independent variable and Ψ_{pd} and Ψ_{mid} as dependent variables. F values for within and between subjects effects are given. Significance of F values are given as $^{**}P \leq 0.01$; $^{***}P \leq 0.001$. Effect size (η^2, in %) for each independent variable is given in parentheses.

Variable	Forest type (FT)	Seasons (S)	Species distribution(SPD)	FT x SPD	S x FT	S x SPD	S x FT x SPD
Leaf water potential$_{pd}$	270.5*** (33.3)	731.9*** (45.4)	25.*** (6.1)	1.2 (0.3)	383.6*** (23.8)	2.4 (0.3)	1.5 (0.2)
Leaf water potential$_{md}$	73.8*** (11.)	893.8*** (49.8)	38.2*** (11.9)	0.8 (0.3)	406.3*** (22.7)	2.4 (0.3)	0.7 (1)
Stomatal conductance	274.2*** (50)	3.0 (0.6)	14.7*** (5.3)	0.5 (0.2)	257.8*** (48.7)	4.7** (1.7)	5.3** (2.0)

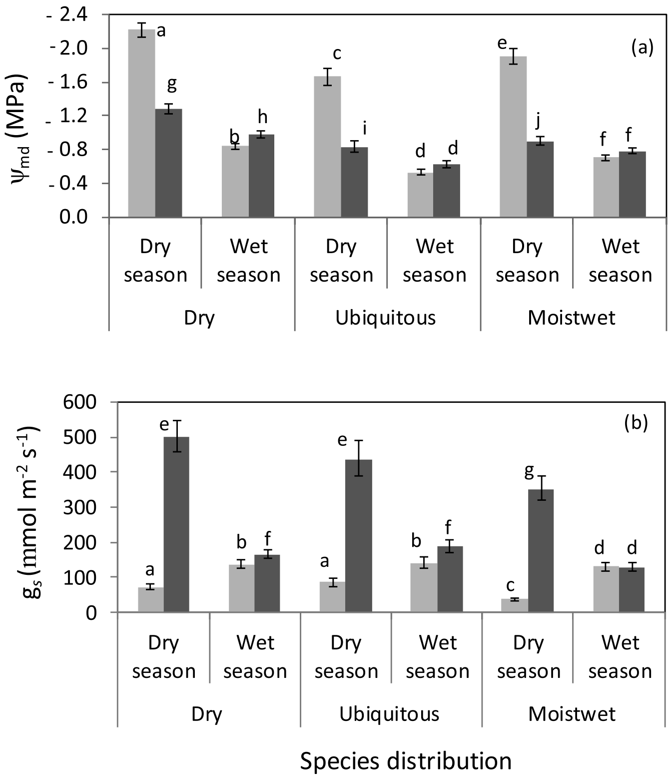


Figure 6. Seasonal variation in leaf physiology among species with different distribution types (dry forest species, ubiquitous species and moist-wet forest species) in dry (grey bars) and wet (black bars) tropical forests. (a) mid-day leaf water potential (Ψ_{mid}) and (b) stomatal conductance (g_s). Means and standard errors are shown. Bars accompanied by different letters are significantly different at $P < 0.05$ (Bonferroni Post-Hoc test).

Species performance in the field and its relation with species rainfall minimum and optimum

Drought survival (i.e., the ratio of survival in the dry forest over survival in the wet forest) in the field and species annual rainfall minimum were significantly negatively correlated (Spearman r = -0.47, P = 0.051, N = 18, Fig. 7a). Survival in the field correlated also significantly negatively with annual rainfall optimum (Spearman r = -0.59, P = 0.010, N = 18, Fig. 7b). This suggests that species that survive relatively well in dry forest compared to wet forest are especially found in drier areas. Similar patterns were shown for the relationship between species growth and the minimum rainfall at which they occurred. The ratio of absolute height growth rate in dry forest over wet forest showed a significant negative relationship with rainfall minimum (Spearman r = -0.47, P = 0.050, N = 18, Fig. 7c). Similarly, the ratio of absolute diameter growth rates in dry forest over wet forest also showed significant negative relationship with a species rainfall minimum (Spearman r = -0.56, P = 0.015, N = 18, Fig. 7d), indicating that species that are naturally distributed at high rainfall areas experience strongly reduced growth under drought stress.

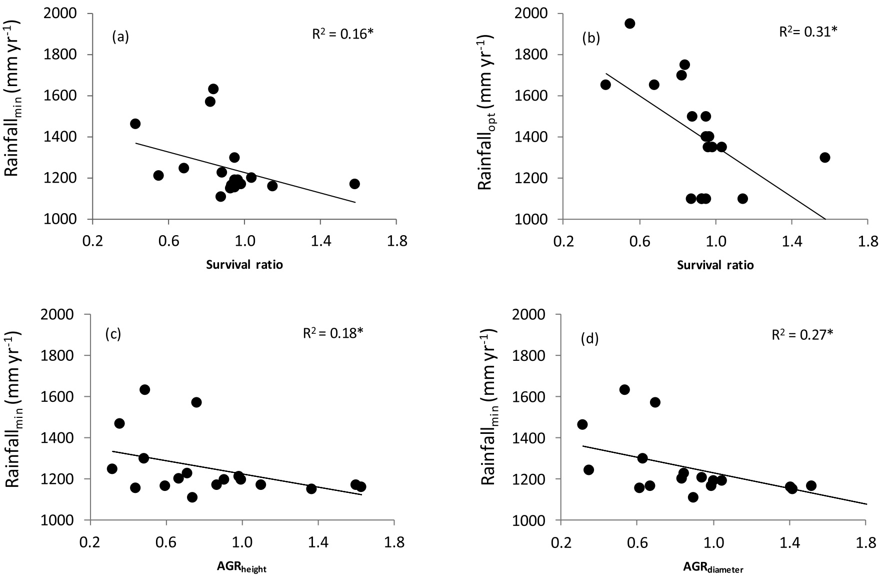


Figure 7. Correlation between species position along rainfall gradient and species drought performance and growth rates in the field. Drought performance in the field was quantified in terms of survival as the ratio of percent survival in the dry forest relative to percentage survival in the wet forest. Survival for each forest was calculated as the number of seedlings surviving at the end of two years relative to number of seedlings alive two months after planting in the field (in %). Growth performance in the field was quantified as the ratio of absolute growth rates in dry forest relative to the absolute growth rates in the wet forest. (a) rainfall minimum and survival ratio, (b) rainfall optimum and survival ratio (c) rainfall minimum and ratio of absolute growth rate of height (AGR_{height}) and (d) rainfall minimum and ratio of absolute growth rate of diameter ($AGR_{diameter}$). Regression lines, coefficients of determination (R^2) and significance level (*: $P < 0.05$) are shown. The correlation is based on 18 species whose response curves were constructed (Amissah *et al.* in press). Inventory data was not available for the other five species; hence their response curves could not be constructed.

DISCUSSION

We investigated seasonal variation in environmental conditions between dry and wet forests and monitored seedling performance (growth and survival) and physiology in these forests. Species relative performance in the field was then related to species distribution along the rainfall gradient. Drought led to reduced physiological activity in the dry season, especially in the dry forest. This led to reduced survival and growth in all species, more strongly so for the wet forest species. Relative drought survival and growth rates in the field were negatively related to species position on the rainfall gradient.

Seasonal variation of environmental conditions in wet and dry forests

We evaluated seasonal variation in environmental conditions between dry and wet forests and found a strong seasonal effect on PAR, temperature, relative humidity and vapour pressure deficit, which varied with forest type. As expected, PAR was higher in the dry forest than in the wet forest and also higher in the dry season than in the wet season. Drought can affect the degree of deciduousness in the canopy which may lead to greater seasonal variation in light transmission and hence variation in PAR (Wright & Cornejo 1990), especially in dry forest where there are more deciduous species (Swaine & Becker 1999). In contrast, in another study in Ghana where PAR was measured along a topographic gradient in wet evergreen and semi-deciduous forests, annual PAR and seasonal fluctuation in irradiance were similar across forest types (Baker *et al.* 2003). In our study, VPD was higher in the dry forests during dry (2.0 kPa) and wet (0.35 kPa) seasons than in the wet forest during dry (0.62 kPa) and wet (0.16 kPa) seasons. Costa *et al.* (2010) also found a larger vapour pressure deficit in the dry season than in the wet season in five Amazonian rain forest sites studied. High temperature and VPD have negative effects on plant carbon balance and plant water status (Jones 1992). Overall increases in dry season temperature and VPD and decreases in RH in both forests lead to increases in evapotranspiration (ET) in the plots. Similarly, evapotranspiration was higher in the dry season than in the wet season in an Amazonian forest (Costa *et al.* 2010). Relative humidity was more pronounced in the dry forest than in wet forest which is in line with the general notion that seasonality plays a much stronger role in determining water availability in dry forests than other factors.

Soil matric potential followed the rainfall pattern and was on average more negative in the dry season at the dry forest (-3.03 MPa) than in the wet forest (-0.43 MPa). Other studies also found more negative soil matric potentials in the dry season (Wright & Cornejo 1990, Veenendaal *et al.* 1996a, Markesteijn *et al.* 2010). Seasonal changes in soil water content causes leaf loss in drought deciduous species (Holbrook *et al.* 1995, Méndez-Alonzo 2013). Wet season soil matric potential were quiet similar in dry (-0.04 MPa) and wet (-0.01 MPa) forests and was near saturation, hence variation in overall growth over the period of the experiment is likely to be more controlled by the length of the dry season and dry season water availability. For example, in a study in Thailand growth was significantly positively correlated with dry-season precipitation levels (Vlam et al. 2014).

Soil from the wet forest was more acidic and lower in N, C and exchangeable cation (Ca, Mg, K and Na) than the dry forest indicating lower fertility of the wet forest soils because of stronger weathering of the bedrock material, and stronger leaching. This finding is similar to results of Veneendaal *et al.* (1996b) where they found lower nutrients levels in wet evergreen forest than the moist semi-deciduous forest. The results also match the differences found in pH and N, K, Ca and Mg between forest ochrosols, that are typical for the wet evergreen forest zone, and forest oxisols, that are typical for the moist-semi deciduous forest zone of Ghana (cf Ahn 1970).

Plant growth and survival

We assessed the seedling performance (growth, survival and physiology) of species with contrasting distributions in dry and wet forests and predicted that there would be a distribution-based home advantage in species performance. In general, growth and survival were higher in the wet forest compared to the dry forest (Fig. 5). Dry forest species indeed had a home advantage, and had higher growth and survival rate than wet forest species in the dry forest, but surprisingly, they also performed better than wet forest species in the wet forest. This may reflect the inherent growth strategy of the species, as most dry species are fast-growing light-demanding pioneers whereas most wet species are slower-growing shade tolerants (Fig. 5). This partially contrasts with the results of Baltzer & Davies (2012) who did a transplanting experiment in "dry" (i.e., seasonal forest with 2-3 months per year < 100 mm rainfall per month, total rainfall 2700 mm/y) and "wet" (i.e. aseasonal forest with no month with less than 100 mm rainfall per month, total rainfall 1950 mm/y) forest in Malaysia. In their study, height and biomass growth rates did not vary between both forest types. Additionally, widespread and aseasonal species performed similarly in the seasonally dry forest. However, in the "wet" forest, wet species had significantly greater relative height growth rates compared with widespread "dry" species (Baltzer & Davies 2012) indicating that wet species have a home advantage. Hence, their study also shows a home advantage for one species group, but not for both, which is in line with our study.

In our study dry and ubiquitous species had higher growth in dry and wet forest than wet species. This is in contrast with findings from a greenhouse experiment of Brenes-Arguedas *et al.* (2008) in Panama, in which "dry"-distribution species (< 2000 mm of rainfall per year) grew on average slower than wet-distribution species (which occur in areas up to 3000 mm of rainfall per year). They attributed the slower growth rates to a cost to drought adaptations. Furthermore, it was hypothesised that inherently slow growth rates of some dry distribution tropical species is one of the main factors limiting their colonization of wetter sites along the rainfall gradient (Brenes-Arguedas *et al.* 2008). Our results do not support this hypothesis, but it should be mentioned that "dry" and "wet" are clearly relative terms, as our Ghanaian forests occur at the lower end of the rainfall gradient, and our "wet forest" is definitely less seasonal, but in terms of annual rainfall only somewhat wetter than the Panamanian "dry forest". It is also possible that distribution based home-advantage could become clearer as species advance in age. Probably at a later age and larger tree sizes, some species may be outcompeted in areas that are not their home range (example, wet forest species may be outcompeted by dry forest species in dry forest and vice versa). In a reciprocal transplanting experiment with a temperate species in Sweden and Italy, there was a strong advantage to local population at the two site used providing a strong evidence of adaptive differentiation of the natural population of the species used (Agren & Schemske 2012).

So what excludes dry species from wet forest areas in Ghana? Our results show that at the seedling stage the low *soil fertility* in the wet forest does not limit the growth of dry species in the wet forest (cf. Baker *et al.* 2003). Similarly, in controlled greenhouse experiments in Ghana and Panama only few species showed a significant growth response to soil fertility and a home-soil based advantage (Veneendaal *et al.* 1996c, Veneendaal & Swaine 1998, Brenes Arguedas *et al.* 2008, L. Amissah *et al.* unpublished data). Furthermore, field transplant experiments neither provided evidence for a home-soil advantage to species with contrasting distribution (Swaine *et al*. 1997, Brenes Arguedas *et al*. 2009). Perhaps nutrient limitation may impede growth when plants advance in age and require more nutrients for rapid growth (cf Baker *et al*. 2003). A supposedly higher *herbivore pressure* in wet forest neither seems to exclude dry forest species in Ghana. Evaluation of herbivore rates (over a period of two months) on the planted 23 species only provided a weak forest effect on herbivore rates (S. Sportel and L. Amissah unpublished data). Additionally, there was little evidence that herbivory could explain the distribution of the tree species (S. Sportel and L. Amissah *et al*. unpublished data). Alternatively, dry forest species may be growing well in wet forest because they have generally a higher *plasticity* than wet forest species. Plasticity in morphological and physiological traits may enhance a plant's ability to avoid conditions that are stressful and use resources when they are available (Grime 1994). The apparent higher growth of dry forest species in wet forest may also be because the experiment was carried out in gaps. If the experiment would have been conducted in the shaded understory the deciduous drought tolerant species would lose their leaves each year, and with the low carbon gain in the understory, they might have problems in replacing the shed leaves. They might also experience higher damage from pathogens in the damp understory, and from herbivores. Wet forest species had less growth and survival in dry forest because they are drought intolerant (Murphy & Lugo 1986). In line with the results of other studies seasonal drought determines the exclusion of wet species from dry forests.

Physiological drought tolerance

We assessed the physiology of seedlings with contrasting distributions in dry and wet forests and predicted that higher vapour pressure deficit in dry forest will lead to more stomatal closure (lower conductance) in dry forest than in the wet forest. We also predicted that dry forest species would have sustained stomatal conductance under a more negative leaf water potential than wet forest species. Season played a significant role in the water status of the plants and this was dependent on the forest type. As predicted, the dry season resulted in a more negative leaf water potential in all species distribution types, especially in the dry forest species (Fig. 6). This was reflected in a lower stomatal conductance during the dry season for all species but conductance was slightly higher in the dry forest species than in the wet forest species. There was neither a home-advantage of species in their physiological response to seasons as there was no forest x species distribution interaction. Result of this study is in agreement with other studies which recorded higher stomatal conductance for all species in the wet season under conditions of high water availability than in the dry season (Choat *et al.* 2006, Craven *et al.* 2011). The dry season was more severe at the dry forest (5 months of less than 50 mm monthly rainfall) compared to two months in the wet forest in the first year of the experiment (Fig. 6). Generally in the dry season transpiration rates are high and the soils in the upper profile are too dry to compensate for increased water demand resulting in more negative water balance in plants, especially those possessing shallow roots (Parolin *et al.* 2010). Additionally, higher vapour pressure deficit and temperature recorded in our experiment during the dry seasons in the dry forest play a large role in determining stomatal conductance, assimilation and therefore carbon balance in plants (Jones 1992, Duff *et al.* 1997, Myers *et al.* 1997). The ability of plants to reduce transpiration and also prevent xylem cavitation by having a higher embolism resistance is key to plant survival and growth in dry environments (Brodribb & Cochard 2009, Kusar *et al.* 2009, Brodribb *et al.* 2010, Choat *et al.* 2012). Drought can markedly decrease physiological activity among seedlings both in field and in controlled studies and hence affect their growth and survival (Parolin *et al.* 2010, Craven *et al.* 2011). In a study in an Indian tropical dry forest, stomatal conductance explained 62% of variability in RGR; an indication of the important role of stomatal conductance in shaping growth patterns across spatial and temporal gradient of soil water availability (Chaturvedi *et al.* 2012).

Species performance in the field is related to species position on the rainfall gradient

Species drought performance (growth and survival) in the dry forest relative to the wet forest correlated significantly with species rainfall minimum and optimum (Fig. 7). Hence, species that performed relatively well in dry forest or under dry conditions tend to occur in drier forest (cf. Engelbrecht *et al.* 2007, Baltzer *et al.* 2008, Poorter & Markesteijn 2008, Sterck *et al.* 2014). These findings suggest that seasonal drought plays an important role in a species' distribution. Additionally, growth in dry forest relative to wet forest was a significant predictor of species position along the rainfall gradient. A modelling study on trees in Spain has shown that growth and mortality are indeed major determinants of species distributions (Garzón *et al.* 2013). However, a modelling study by Sterck *et al.* (2014) found that species distribution along the rainfall gradient was not related to the growth potential of the species, but to species survival under suboptimal conditions (i.e., their water compensation point).

In our study system, dry forest species performed better than wet forest species in the wet forest, indicating that in the first two years of establishment in gaps, seedlings of dry forest species tolerate high water availability, potentially high pest pressure and low soil nutrients in the wet forest. Such performance can be attributed to higher plasticity of dry forest species as indicated by a higher survival and growth ratio (Fig. 7). Although most forest species have been found to show a narrow hydraulic safety margin (< 1 MPa) under severe drought stress regardless of mean annual rainfall under which they are found (Choat *et al.* 2012), wet forest species are likely to show a much narrower hydraulic safety margin and will be excluded from dry environment when soil drought become frequent and severe. It is important to note that overall, we did not find species distribution-based home advantage in growth and survival within the experimental period of two years. Nevertheless, it is likely that plant will show a home advantage over the course of time, or at a later age when demand for resources increase when plants increase in size.

CONCLUSIONS

Drought reduced the physiological activity and growth of plants. This growth reduction was more pronounced in the dry forest where seasonal variation in environmental conditions (soil matric potential, temperature, and VPD) is large. In the rainy season soil matric potential was similar in both dry and wet forests, but wet forest plants had a higher stomatal conductance, and hence a higher carbon gain and growth. Dry forest species had a home advantage and realized higher growth and survival in the dry forest compared to wet forest species. The drought survival in the dry forest relative to the wet forest was significantly related to species position on the rainfall gradient, which indicates that seasonal drought plays an important role in shaping species distribution. Hence, seasonal drought in combination with inherent growth characteristics and plasticity are among the major factors shaping the distribution of these tree species.

ACKNOWLEDGEMENTS

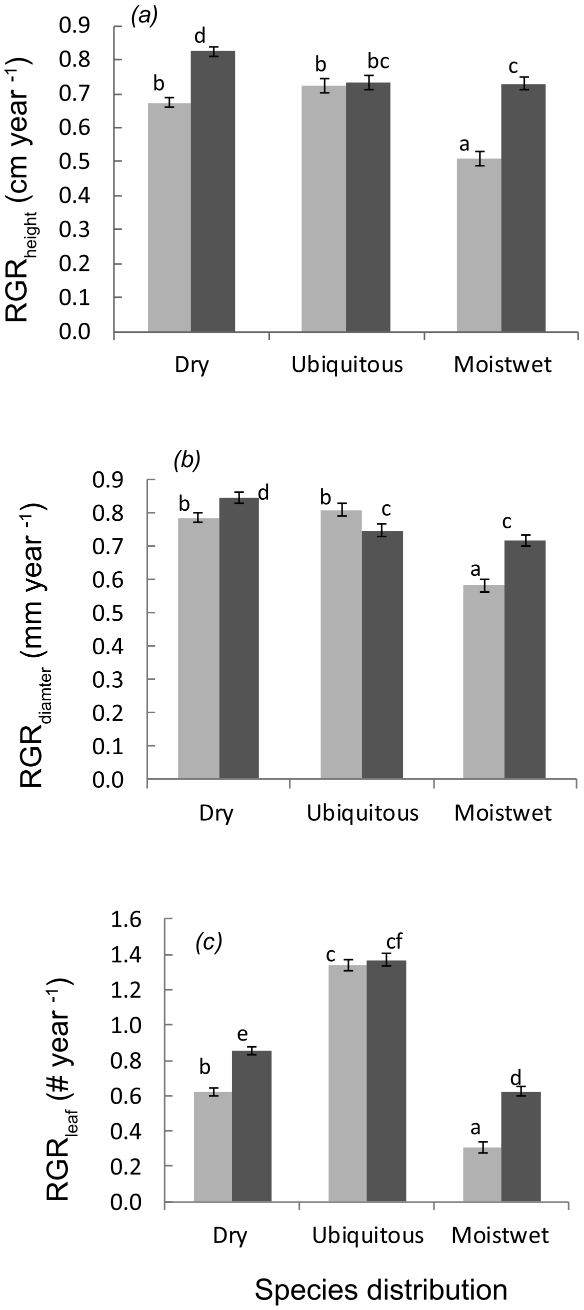
The authors thank Netherlands Fellowship Programme (Nuffic), Wageningen University and the Council for Scientific and Industrial Research- Forestry Research Institute of Ghana (CSIR-FORIG) for providing funding for the study, and Peter Amoako, William Hagan–Brown, Elvis Nkrumah and Nana Prempeh Bandoh for assistance with data collection.

Appendix 1. List of species, abbreviations, family, guild and forest type. Species' family name, guild and forest types are according to (Hall and Swaine 1981, Hawthorne 1995, Hawthorne & Jongkind 2006a, Hawthorne and Ntim Gyakari 2006b). NPLD = Non-pioneer light demander. *= species whose response curves are not available.

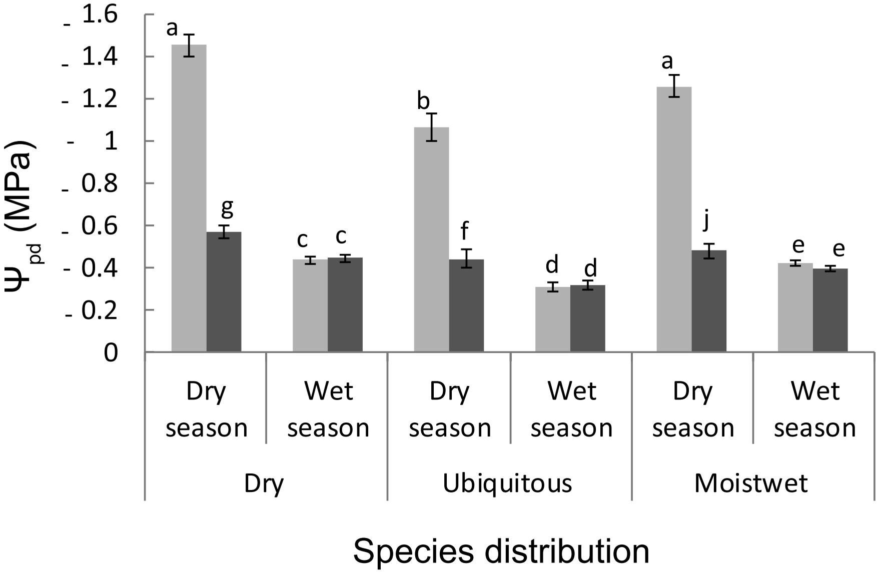
Species	Family	Species guild	Forest type
Heritiera utilis	Sterculiaceae	NPLD	Wet
**Lophira alata*	Ochnaceae	Pioneer	Wet
**Khaya ivorensis*	Meliaceae	NPLD	Wet
Pentadesma butyracea	Caesalpinaceae	Shade tolerant	Wet
Entandrophragma angolense	Meliaceae	NPLD	Moist
Turraeanthus africanus	Meliaceae	Shade tolerant	Moist
**Tieghemella heckelii*	Sapotaceae	NPLD	Moist
Terminalia ivorensis$_{Wet}$	Lecythidaceae	Pioneer	wet
Piptadeniastrum africanum	Mimosaceae	NPLD	Moist
Ricinodendron heudelotii	Euphorbiaceae	Pioneer	Dry
Newbouldia laevis	Bignoniaceae	Pioneer	Dry
Mansonia altissima	Sterculiaceae	NPLD	Dry
Nesogordonia papaverifera	Sterculiaceae	Shade tolerant	Dry
Ceiba pentandra	Bombacaceae	NPLD	Dry
**Celtis zenkeri*	Ulmaceae	NPLD	Dry
Albizia zygia	Mimosaceae	NPLD	Dry
Pericopsis elata	Papilionaceae	NPLD	Dry
Sterculia rhinopetala	Sterculiaceae	NPLD	Dry
**Khaya anthotheca*	Meliaceae	NPLD	Dry
Antiaris toxicaria	Moraceae	NPLD	Ubiquitous
Strombosia pustulata	Olacaceae	Shade tolerant	Ubiquitous
Terminalia ivorensis$_{dry}$	Combretaceae	Pioneer	Ubiquitous
Terminalia superba	Combretaceae	Pioneer	Ubiquitous

Appendix 2. Acidity and nutrient concentrations and mechanical properties of soils of two contrasting forest sites (dry forest and wet forests) in Ghana.

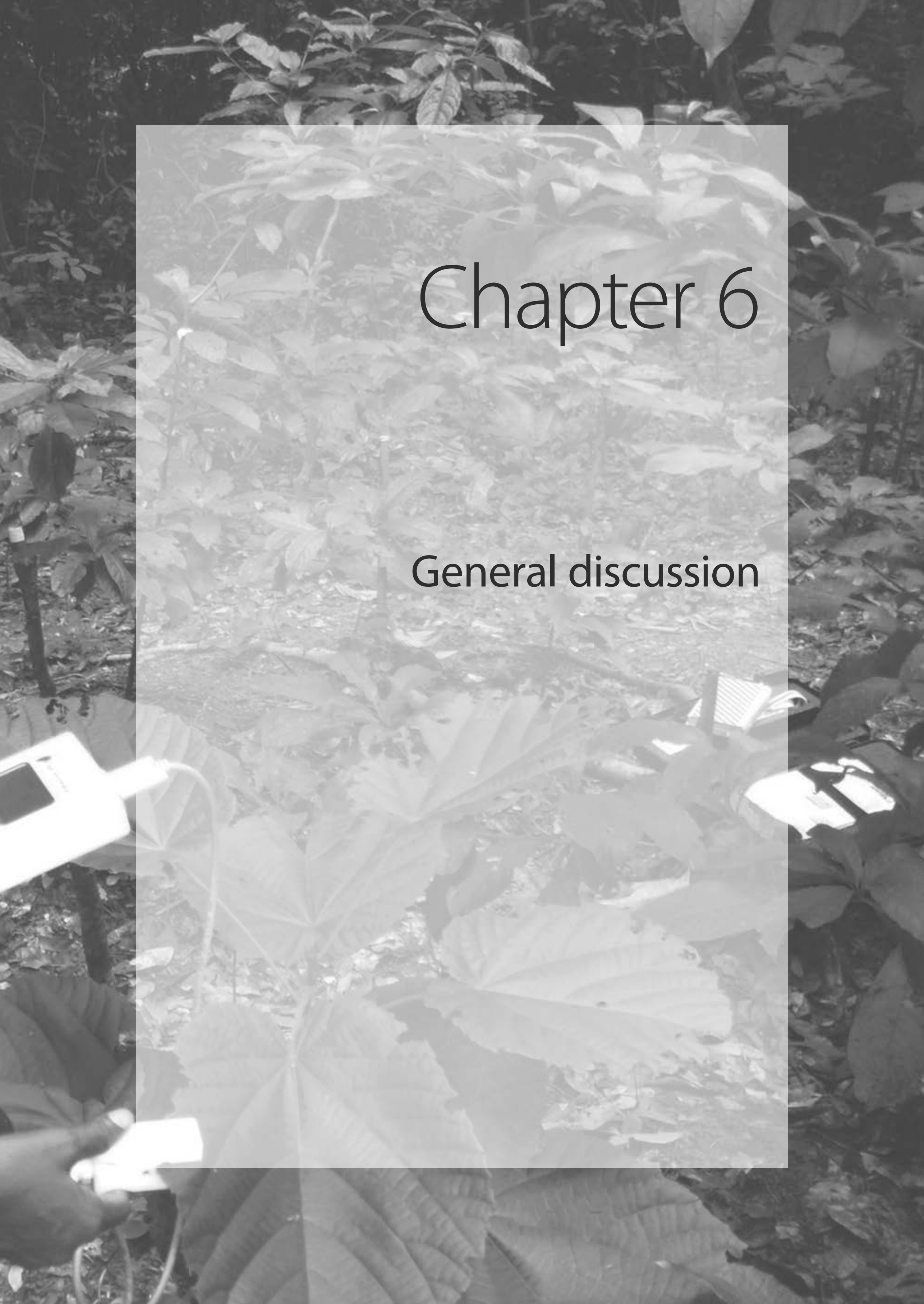
Soil nutrients and texture	Dry forest	Wet forest
pH (H_2O 1:1)	6.20	4.88
Carbon (%)	1.97	1.75
Nitrogen (%)	0.18	0.14
Organic matter (%)	3.40	3.02
Exchangeable Cation		
Ca (Cmol/kg)	8.54	1.60
Mg (Cmol/kg)	3.20	0.53
K (Cmol/kg)	0.15	0.08
Na (Cmol/kg)	0.05	0.03
TEB Cmol/Kg	11.94	2.24
ECEC (Cmol/Kg)	12.04	3.09
Base Saturation (Cmol/Kg)	99.17	72.49
Available		
P (ppm)	4.94	3.75
K (ppm)	62.90	34.15
Mechanical properties		
Clay (%)	22.40	20.20
Sand (%)	23.74	15.56
Silt (%)	53.86	64.24
Gravel content	-	42.22%
Texture type	Silty loam	Silty loam



Appendix 3. Relative growth rates of species with different distributions (dry species, ubiquitous species and moist-wet species) in dry (grey bars) and wet (black bars) tropical forests at the end of the 2-year period. (a) Height, (b) diameter and (c) number of leaves. Means and standard errors are shown. Bars accompanied by different letters are significantly different at $P < 0.05$ (Bonferroni Post-Hoc test).



Appendix 4. Seasonal variation in predawn leaf water potential (Ψ_{pd}) among species with different distribution types (dry species, ubiquitous species and moist-wet species) in dry (grey bars) and wet (black bars) tropical forests. Means and standard errors are shown. Bars accompanied by different letters are significantly different at $P < 0.05$ (Bonferroni Post-Hoc test).



Chapter 6

General discussion

INTRODUCTION

Tropical forests occur along a rainfall gradient in which light availability at the forest floor decreases with increasing mean annual rainfall because the canopy of wet seasonal forests is dense and more closed, whereas the canopy of dry seasonal forests is sparse and more open. Pest pressure increases with mean annual rainfall because the population of herbivorous insect pests is reduced during the dry season (Wright 1992, Coley 1998, Engelbrecht *et al.* 2007, Arguedas *et al.* 2009, Brenes-Arguedas *et al.* 2011). Additionally, the soil nutrient content tends to decrease with increasing mean annual rainfall, because of increased leaching (Swaine 1996). Interaction among some of these factors and other disturbance regimes such as fires influences the establishment (growth, survival) and distribution of tree species along the rainfall gradient (Hawthorne 1994, Burslem 1996, Brenes-Arguedas *et al.* 2011, conceptual diagram Fig 6.1).

Recent studies indicate that the effect of soil and pests on tree species distribution is relatively minor compared to the effects of water availability (Brenes-Arguedas *et al.* 2009, Baltzer & Davies 2012). Furthermore, drought performance and physiological drought tolerance have been found to determine the distribution of tropical tree species (Engelbrecht *et al.* 2007, Baltzer *et al.* 2008, Poorter & Markesteijn 2008). This suggests that changes in the availability of water in tropical forest may affect the distribution of tropical tree species, especially of those species that occur at the wetter end of the rainfall gradient (Engelbrecht *et al.* 2007).

Light availability at the forest floor varies along the rainfall gradient and is thought to act in combination with water availability to determine the establishment, growth and survival of species (Fisher *et al.* 1991, Veenendaal *et al.*1996a). High light may exacerbate the impact of drought because when light availability is high but water availability is low, the performance (in terms of growth and survival) of plant species is strongly reduced (Sack 2004). Young seedlings may be more vulnerable to a reduction in rainfall because their small root system does not allow them to forage for water in deeper and wetter soil layers. However, the capacity of tropical tree species to respond to low water availability is poorly understood (Feeley *et al.* 2007, Wright 2010, Corlett, 2011). Understanding the responses of species to current environmental factors may give insight into how species may respond to future changes in the climate (e.g. in rainfall). Furthermore, information on the mechanisms underlying species' responses may enhance the predictive ability of models that are used to forecast the impact of climate change on forests. Only a few studies (see Fisher *et al*. 1991, Burslem 1996; Veenendaal *et al*. 1996a) have evaluated the combined effects of drought and shade (low light) on relative growth rates, plants morphology and biomass allocation to leaves and roots. As these studies were on few species, generalisation of their findings is more difficult.

In this thesis, I used forest inventory data, a greenhouse experiment and a field experiment to study the factors that influence the distribution of 10-23 tree species' and the underlying mechanisms. The dissertation aims to provide additional insight into the relative importance of climatic factors to the distribution of individual species. Furthermore, physiological and morphological acclimatisation, plasticity to drought and shade, and the functional traits that predict drought survival and distribution of species were analysed. The main focus was on plant drought adaptation strategies and how drought performance relates to distribution of species. This general discussion chapter highlights the major findings reported in the various chapters and their linkages, and focuses on four major questions: (1) What is the relative importance of rainfall and temperature on tree species distribution? (2) How do tree species acclimatise to drought and shade in terms of their physiology, morphology, growth and survival? (3) What morphological and physiological traits determine species drought performance and distribution? (4) How do seedling survival, growth and physiology in the field vary between dry and wet forests, and does drought tolerance and growth determine species distribution along the rainfall gradient? Below I discuss the ecological and management implications of the study results and make recommendations for species selection in reforestation efforts and strategies for climate change mitigation.

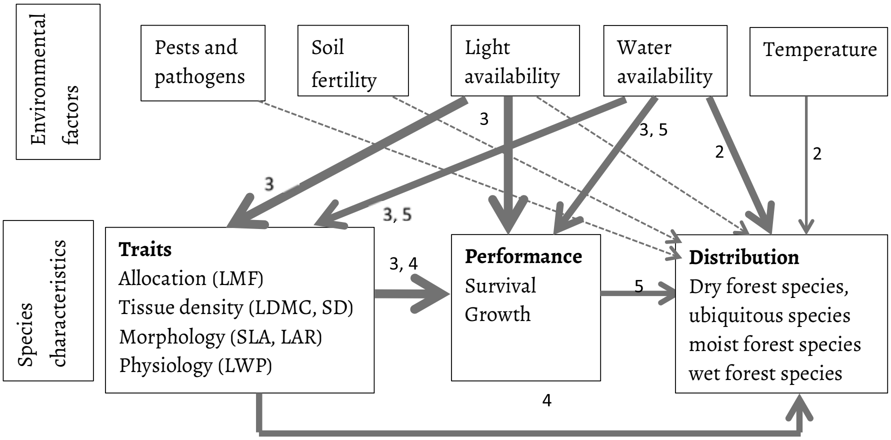


Figure 6.1 Conceptual framework of how environmental factors and species traits together shape the performance and distribution of tree species. The width of the arrows indicates the strength of the relationship found in this study. The numbers next to the arrows indicate the chapter of the thesis that addresses the specific issue. The most important traits affecting species performance and distribution are shown. These are related to allocation (LMF = leaf mass fraction), tissue density LDMC = leaf dry matter content, SD = stem density), morphology (SLA = specific leaf area), and physiology (LWP = leaf water potential). Species distribution has been analysed as a continuous variable (as the rainfall minimum under which the species occurred, Chapter 2), and as a categorical variable; as species distribution types (dry forest species, ubiquitous species, and moist/wet forest species). The dotted arrows are factors that co-shape species distribution but for which the results are not presented in this thesis. High LMF reduces species drought survival, high LDMC and SD increase species drought survival. Species with high SLA and LAR occur at the wetter end of the rainfall gradient, where light is a limiting factor. Ubiquitous = occurring in all forest types in Ghana , "dry", "moist" and "wet" describe wetness. That is dry forest, moist forest and wet forest of Ghana.

1. Relative importance of rainfall and temperature for species distribution (Q1)

In Chapter 2 of this dissertation I evaluated the relative importance of four climatic factors for the distribution of 20 tree species. The study showed that virtually all species (95%) responded to rainfall amount, whereas 60% responded to rainfall seasonality (Chapter 2, Fig. 2). Together, rainfall and rainfall seasonality explained 22% of the variation in species occurrence. Several studies (Hall & Swaine 1976, 1981, Gentry 1988, Swaine 1996, Condit 1998, Bongers *et al.* 1999, Engelbrecht *et al.* 2007, Toledo *et al.* 2012, Condit *et al.* 2013) have found rainfall and rainfall seasonality to be the best predictors of species distribution. In my study, temperature explained, on average, much less variation (5%) in species occurrence and was mostly associated with decreasing (4 out of 20 species) response and unimodal (4 out of

20 species) response. These findings underscore the importance of temperature for the distribution of some species. Indeed, recent studies suggest that small changes in temperature may have large impact on tropical species (Wright *et al*. 2010). Field studies on tropical trees in Costa Rica, Panama and Thailand reported that at high temperatures growth was poor (Clark *et al*. 2003, Feeley *et al*. 2007, Vlam *et al*. 2014). A possible explanation for this negative relationship is that at high temperatures, autotrophic respiration rates are enhanced and hence photosynthetic rate is compromised (Clark 2007, Feeley et al. 2007, Galbraith et al. 2010). At higher ambient temperatures, the maintenance costs of plant tissue increase (Lloyd & Farquhar 1996). In combination, the four climatic factors I studied explained on average less than 40% of the variation in species occurrence, which suggests that the distribution of species is shaped by other non-climatic factors (e.g. pests, soil, vegetation history, dispersal limitation and chance events). I found that the 20 species showed different response curves to the four climatic factors studied (Chapter 2, Table 2). Several other studies have also found inter-species differences in the response curves of species to environmental gradients: Oksanen & Minchin (2002), Lawesson & Oksanen (2002), McKenzie *et al.* (2003) in temperate forest and Bongers *et al.* (1999), Toledo *et al.* (2012) in tropical forest. Such response curves provide a basis for the selection of species for drought or temperature tolerance screening. Such a drought screening study was conducted in Chapter 3 of this dissertation and is discussed in the next section.

1.1 Environmental conditions in dry and wet forests

The diversity of tropical tree species, their composition and distribution in tropical forests are largely shaped by the amount of rainfall, length and intensity of the dry season and other associated environmental resources and conditions (Bongers *et al*. 1999, Condit *et al*. 2013, Swaine & Becker 1999. In Chapter 5 of this dissertation I assessed seasonal variation in environmental conditions in dry and wet forest sites (summary in Fig. 6.2). I found that water availability (quantified as soil matric potential) in the dry season was on average lower in the dry forest sites than in the wet forest (-3.03 MPa versus -0.43 MPa) (Chapter 5, Fig. 4a, b). This was also due to the difference in duration of dry season, which was 4 months in the dry forest and only 1.5 months in the wet forest (Chapter 5, Fig. 2). Other factors that may influence plant water availability and drought stress include soil texture, higher evaporative demand, higher transmission of photosynthetically active radiation (PAR), and associated high temperature and vapour pressure

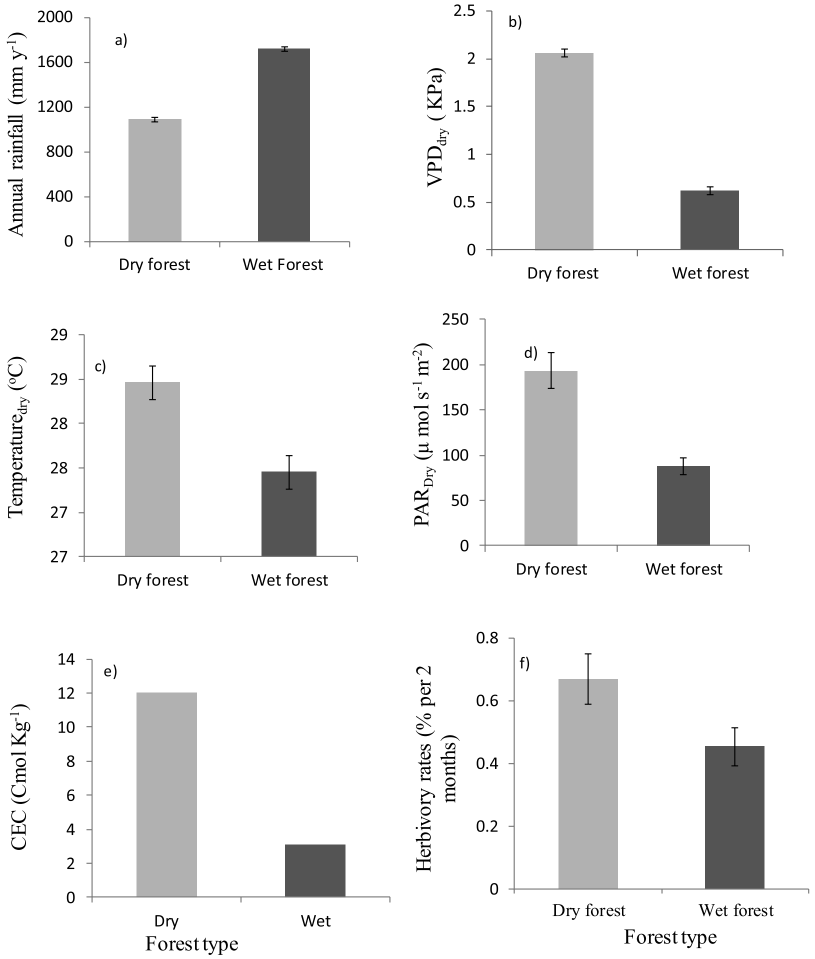


Figure 6.2. Summary of environmental conditions in dry and wet forests of Ghana. The Environmental and climatic variables were all measured in two dry seasons (January 2012 and January 2013) at the two study sites: Afram Headwaters Forest Reserve and Neung South Forest Reserve. Herbivory was measured on saplings by S. Sportel and L. Amissah and the data are not included in this thesis. (a) mean annual rainfall, (b) vapour pressure deficit (VPD) during the dry season, (c) mean air temperature during the dry season, (d) photosynthetically active radiation (PAR) during the dry season, (e) cation exchange capacity (CEC) of the soil and (f) herbivory rates.

deficit (VPD) (Wright & Cornejo 1991, Costa *et al.* 2010, Markesteijn 2010). As Chapter 5 Fig. 3a, b, d, Fig 6.2 b, d show, in the dry season we did indeed find higher values for average PAR and VPD in the dry forest than in the wet forest: average PAR was 192 µ mol m^{-2}s^{-1} versus 88 µ mol m^{-2}s^{-1}, Fig 6.2d and average VPD was 2.06 kPa versus 0.62 kPa, Fig. 6.2 b. High temperature and VPD have negative effects on plant carbon balance and plant water status (Jones 1992). The soil texture in the two forest categories was similar, except that the soil in the wet forest contained a high percentage (42.22%) of gravel (Appendix 2). Soil in the wet forest was more acidic (pH = 4.88) than in the dry forest (pH = 6.20). Additionally, soil fertility (e. g. cation exchange capacity) was lower in the wet forest soil (3.09 cmol kg^{-1}) than in the dry forest soil (12 cmol kg^{-1}). Low soil fertility may limit plant growth and the recruitment of species with high nutrient requirements in wet forest. Indeed, the distribution of species in moist tropical forest has been found to be associated with soil fertility (Wright 1992, Swaine 1996). The temporal and spatial variation in environmental conditions in tropical forests together with differences in species responses may result in niche differentiation and coexistence of species.

2. How do species acclimatise to drought and shade (Q2)?

2.1 Species drought and shade performance

The differential ability of plants to survive and grow under stressful conditions in the forest environment determines the future composition and structure of the forest canopy (Burslem 1996). In this study, I demonstrated that drought reduces the survival of species both under experimental drought in the greenhouse, and in the field, especially in the dry forest. Seedling survival over a nine-week experimental drought in the greenhouse (20% sunlight) was lower than that of seedlings in the field (gaps of ca. 20% sunlight) over two years (including two dry seasons): 21.4% versus 79.6%. The difference is statistically significant (Mann-Whitney test $U = 44.0$, $Z = -4.8$, $P < 0.001$). A possible explanation for the higher survival in the field is that field plants had access to a large volume of soil and therefore to more available water than the plants growing in a small volume of soil in the pots (Poorter *et al*. 2012). At the end of the rainy season, plants in the field had large size and their roots could therefore explore a larger soil volume for water, and explore deeper soil layers in which more water tends to be available in the dry season. The lower survival in the greenhouse cannot be attributed to the ambient temperature being higher than in the field, because the average temperature in the greenhouse was similar to the field temperature in the dry forest (ratio = 1.02). Also, the relative humidity in the 20% sunlight greenhouse was on average 70.3% compared to 46.8% in the dry forest during the dry season (Table 6.1). Seven of the 24 species (mostly the ones occurring in dry forest and those that were ubiquitous (i.e. occurring in all forest types) had a survival rate of over 50% in the greenhouse (Chapter 4, Fig. 2); in the field, 22 of 23 species had a survival rate of ≥ 50% over the two-year period including two dry seasons (Chapter 5, Fig. 5d). This also indicates that some tropical tree species are well adapted to drought conditions (cf. Engelbrecht & Kusar 2003). For example, in Panama, mortality of seedlings of three common shade-tolerant tree species did not increase in response to a severe El Niño when compared to seedling mortality in normal years (Engelbrecht *et al.* 2002).

In the greenhouse, shade facilitated survival: drought survival in low light (5% of full sunlight) was 89% compared to 53% survival in the high light (20% of full sunlight). Similar findings have been reported by others (Holmgren *et al.* 2000, Moreno & Oechel 1992, Sack 2004). Normally, shade conditions lead to lower air temperatures, low vapour pressure deficits and hence less drought stress (cf. Thomas & Davis 1989, Holmgren *et al.* 2000, Sack 2004). Yet in the greenhouse experiment, the temperature and relative humidity in the greenhouse with 5% sunlight and in the greenhouse with 20% sunlight were similar (Chapter 2, appendix 2). The higher drought survival in the low light greenhouse can therefore be attributed to the soil water reserve in the pot being depleted more slowly because of a combination of smaller seedlings with smaller transpiring leaf area, lower transpiration rates per unit leaf area and less water evaporation from the soil. These results support the hypothesis that although understory species in the forest face competition for water from the canopy trees, they will be able to survive seasonal drought (Sack 2004). Our finding that drought had more effect on growth rates in the greenhouse with 20% irradiance than on the growth rates in the greenhouse with 5% irradiance (Chapter 3 Fig 1a, b) contrasts with the findings of Sack and Grubb (2002) and Sack (2004), who reported a proportional reduction of RGR in low light and high light (i.e. no interaction effect).

Table 6.1 Temperature and relative humidity in greenhouse and field (dry forest and wet forest of Ghana) experiments.

	Greenhouse 20% light		Greenhouse 5% light	
Experiment	Temperature (°C)	Relative humidity (%)	Temperature (°C)	Relative humidity (%)
Greenhouse batch 1	28.0	76.0	28.0	77.01
Greenhouse batch 2	30.4	64.5	30.5	65.2
Dry forest dry season	28.5	46.8		
Wet forest dry season	27.5	83.3		
Dry forest wet season	24.7	88.9		
Wet forest wet season	26.6	95.4		

2.2 Species morphological and physiological acclimation to drought and shade

The water stress a plant experiences depends on the plant's physiological and morphological characteristics (Poorter & Hayashida-Oliver 2000). Plants show different levels of acclimatisation to different environments. Acclimatisation is the phenotypic plastic response of a genotype to different environmental conditions. Plants maximise their surface area to capture the most limiting resource (Brouwer 1963). For instance, plants growing in shade invest in high aboveground biomass (leaves and stem) and also produce thin leaves to optimise light capture and use (Reich *et al.* 1998, Evans & Poorter 2001, Gommers *et al.* 2013). According to Smith & Huston (1989) plants growing in shade allocate more biomass to leaves and less to roots, resulting in a trade-off between survival in shade and survival in drought. The findings reported in Chapter 3 support these contentions: first, species in shade (5% of full sunlight) allocated more biomass to leaves, to capture more light, but this was at the expense of allocation to roots, which suggests a trade-off as hypothesised by Smith & Huston (1989) (Chapter 3, Fig. 2 a, g). However, plants growing in shade also produced thin roots (high specific root length, SRL) that compensated for the lower biomass investment in roots. This could be a strategy that allows shaded plants to acquire enough water whilst at the same time enhancing light capture through a higher biomass investment in leaves (leaf mass fraction, LMF), the production of thin leaves (high specific leaf area, SLA) and leafier plants (high leaf area ratio, LAR). The second supportive finding is that plants growing under drought allocated more biomass to roots (Fig. 2g), but surprisingly they did not reduce their biomass allocation to leaves (Fig. 2d), nor did they change their biomass allocation in stem. Neither did droughted plants produced thin roots (high SRL, Fig. 2 h) that could enhance water uptake. Other studies have shown that seedlings growing under drought stress or low rainfall areas have low SLA and LAR which help to reduce transpirational water loss (Fonseca *et al.* 2000, Poorter & Markesteijn 2008).

Plant phenotypic plasticity may be vital for species to adjust to temporary and spatial variation in resource availability. The capacity of plants to exhibit plastic responses to environment is one factor that defines a species' ecological breadth (Saldaña *et al.* 2005). I expected plants with plastic traits to be flexible to environmental variation and therefore to grow and survive well. However, contrary to my expectations, neither growth nor survival was significantly related to overall plant plasticity (the change in the characteristic of an individual plant to changes in environmental condition), calculated for 9 traits across all four light and water treatment combinations (Chapter 3, Table 3). I found, however, that plasticity in root mass fraction (RMF, root mass divided by plant mass) was positively related to growth rate (Chapter 3, Table 3, and Fig. 4 d). Plasticity in leaf mass fraction (leaf mass divided by plant mass) was also positively related to drought survival (Chapter 3, Fig. 4b), which suggests that the plant may be adjusting to changes in the environment by adjusting its biomass allocation patterns instead of its morphology. In the field (Chapter 5, Fig. 7) plasticity in growth and survival (calculated as growth or survival in the dry forest relative to the wet forest) was negatively related to a species' minimum rainfall of occurrence (that is the minimum mean annual rainfall on the rainfall gradient at which a species occurs), indicating that species growing in drier environment are more plastic and have higher survival under water stress than species growing in the wetter environment. However, we found that plasticity in survival was not significantly related to other species distribution characteristics, such as the rainfall range (computed as the difference between the minimum mean annual rainfall and the maximum mean annual rainfall at which a species occurs (Chapter 2).

Physiological responses: Drought can significantly decrease physiological activity among seedlings growing in the field and in controlled environment and hence influence their growth and survival (Parolin *et al.* 2010, Craven *et al.* 2011). Seedling physiological adjustment in the field (Chapter 5, Figs 6 a, b) was similar to that in the greenhouse (Chapter 3 Fig. 3 a, b). My finding that in both dry and wet forests in the field, and greenhouse drought reduced leaf water potential and stomatal conductance (Chapter 5, Figs 6a, b) is consistent with the results of other studies (Choat *et al.* 2006, Craven et *al.* 2011). In my study, dry forest species had more negative midday leaf water potential (Ψ_{md}) than the ubiquitous species and wet forest species across dry and wet seasons; such capacity to tolerate low leaf water potential has been found to determine the drought survival and distribution of tropical tree species (Engelbrecht *et al.* 2007, Baltzer *et al.* 2008, Kusar *et al.* 2009, Chapter 5, Fig. 6a). Plants tolerating lower leaf water potentials are able to keep their stomata open and to sustain hydraulic conductivity for longer (Tyree et al. 2003). In some plants, seasonal drought stress limits the length of time that the stoma remains open during the day, and thereby causes daily rates of carbon assimilation to decline (Chaves *et al.* 2002), resulting in less growth. For example, in a dry tropical forest in India, Chaturvedi *et al.* (2012) found that stomatal conductance explained over 62% of variation in relative growth rates. They argued that this provides more evidence for the role of leaf water stomatal conductance in shaping growth patterns across spatial and temporal gradients in soil water availability.

2.3 Is there a trade-off between drought survival and shade survival?

A *trade-off* has been reported between drought survival (i.e. drought tolerance) and shade survival (i.e. shade tolerance) both across and within species, due to a trade-off between the allocation of biomass to leaves and to roots (Huston & Smith 1989, Niinemets & Valladares 2006, Poorter and Markesteijn 2008). Allocation to leaves facilitates light capture and hence shade survival, whereas allocation to roots facilitates water capture and hence drought survival. I found interaction effect between light and water in 40% of the traits studied, including relative growth rates. In plants growing under high light, reduction in growth in response to drought was stronger than in plants growing in low light. Drought survival was also reduced more in plants growing in high light (Chapter 3, Fig.1 a, b). A significant drought–light interaction indicates that the effect of one factor (e.g. drought) on a variable (e.g. RGR) depends on another factor (e.g. shade). The effects of the two factors are therefore not additive, which implies that the effects of drought and shade follow different pathways. In extreme cases, such interaction may indicate a trade-off (for example, one factor may cause the dependent variable to increase, whereas another factor causes it to decrease). Generally there were no trade-offs (defined as interaction between light and water effects on 12 morphological and physiological traits and relative growth rates) in 60 % of traits studied (Chapter 3, Table 2), which suggests that the effect of drought is not coupled with the effect of shade. This independence of shade and drought responses has been found in earlier studies, most of which were conducted in temperate areas (Sack 2004, Sack and Grubb 2002) and implies that species have an opportunity for niche differentiation and coexistence under a range of water and light conditions.

3. What morphological and physiological traits (functional traits) determine species drought performance and distribution (Q3)?

A functional trait is any characteristic which impacts plant fitness indirectly through its effects on growth, survival and reproduction (Violle *et al.* 2007). A number of tropical studies have demonstrated a relationship between traits, growth, and species coexistence (see Poorter & Bongers 2006, Kraft *et al.* 2008, Wright *et al.* 2010) but few studies (Poorter & Markesteijn 2008, Kursar *et al.* 2009, Brenes-Arguedas *et al.* 2013) have linked traits to the drought survival and drought strategies of tropical trees. In this study, I showed that plant species exhibit three main drought strategies: (1) drought avoidance, (2) drought delay and (3) physiological drought tolerance. These drought strategies are influenced by a suite of traits. Drought avoidance is controlled by deciduousness: deciduous species shed their leaves during the dry season to reduce water loss (Borchert 1994). Drought delay is controlled by traits that enhance access to water (e.g. deep roots) and reduce water loss through stomatal control (Quero *et al.* 2011). Physiological drought tolerance involves the ability to function physiologically (e.g. stem water transport) even at low leaf water potential (Tyree *et al.* 2003, Kursar *et al.* 2009).

In Chapter 4, I evaluated the traits that best predict drought survival. Drought survival was predicted by a suite of traits related to biomass allocation to leaves and roots and, tissue density (Chapter 4, Table 3). I reported that leaf mass fraction (total leaf mass divided by plant mass) was negatively related to drought survival (Chapter 4, Fig. 3a). For example, plants that had less leaf mass than root mass and stem mass had higher survival. Less allocation to leaves helps plants to reduce the transpiration load, especially in an environment with a high vapour pressure deficit and low soil water availability. The leaf dry matter content (dry mass per unit fresh mass x 100, LDMC) was positively related to drought survival. High LDMC indicates structurally reinforced and dense leaves, which allow plants to adjust their leaf water potential to very low levels in drought-stressed environments (Niinemets 2001). Tolerance of low leaf water potential (LWP) is correlated with drought survival and hence with species distribution (Kursar *et al.* 2009, Baltzer *et al.* 2008). In my study, leaf water potential (LWP) at the moribund stage (at the nearly dead stage) was not related to drought performance but we found a moderate positive correlation between LDMC and the LWP under the slightly wilted stage (Chapter 4, $r = 0.52$, $P \leq 0.01$, $n = 24$), and at the moribund stage (Chapter 4, Fig. 5). Engelbrecht & Kursar (2003) found that midday leaf water potentials of saplings of four species measured during a dry season in Panama also did not show any relationship with drought survival; this implies that drought survival is controlled by a suite of traits. In Chapter 4 (Fig. 3d) I showed that drought survival was positively associated with stem density (cf. Poorter & Markesteijn 2008). The denser the stem the better the hydraulic safety because plants with high stem density have narrow vessels and pit pores and resist xylem embolism even under low xylem potential (Choat *et al.* 2012, Jacobsen *et al.* 2007, Lens *et al.* 2013, Markesteijn *et al.* 2011, Méndez-Alonzo *et al.* 2012). High leaf dry matter content is related to physiological drought tolerance (Chapter 4, Fig. 5), and low leaf mass fraction is associated with drought delay. Overall the results of our study indicate that *drought delay* is an important component of a drought survival strategy.

Plant **traits** determine the **distribution** of species because they determine the survival and growth of species (Westoby & Wright 2006). It therefore seems probable that the traits of a species are related to the distribution of that species. This study showed that SLA is negatively related to a species rainfall minimum (Chapter 4, Fig.4, and Table 6.2): species from a wet environment had low SLA. This is in contrast to the findings of other studies, which have reported a lower SLA for species growing in dry environments (Carter, Theodorou & Morris 1997, Milla *et al.* 2008). One possible explanation for the relation I found in this study is that some species that grow in dry areas shed their leaves in response to drought and should normally have a high SLA to maximise growth during the growing seasons (Ruiz-Robleto & Villar 2005). However, most of our study species (e.g. *Mansonia altissima, Newbouldia laevis, Sterculia rhinopetala, Celtis zenkeri)* are evergreen. The lower SLA associated with wet forest species may be related to adaptations to other environmental factors (e.g. pests) rather than to drought. Lower SLA enhances the plant's defence against insects (Kitajima & Poorter, 2010) and pathogens, which occur more frequently in wet environments. Reducing tissue loss is especially important in the shaded forest understory, where carbon accumulates slowly in plants (Kitajima & Poorter, 2010). Low SLA is also associated with shade tolerance (Kitajima 1994, Poorter & Bongers 2006) and tolerance to nutrient-poor soils (Aerts 1999, Baltzer & Thomas 2010). SLA is one of the major traits contributing to the 'primary axis of specialization' (Grime *et al.* 1997) and the global leaf economics spectrum (Wright *et al.* 2004). It has also been found that SLA determines species distribution along a nutrient gradient

(Phillips *et al.* 2003), a water gradient (Bongers *et al.* 1999, Ackerly 2004), and a light gradient (Ackerly *et al.* 2002) at large spatial scales and, during secondary succession, at large temporal scales (Krober *et al.* 2012, Lohbeck *et al.* 2013). In my study, three traits (LMF, LDMC and RDMC) predicted both drought survival and a species' mean annual rainfall minimum. However, the most important predictor trait for drought survival and the most important predictor trait for a species position on the rainfall gradient were not the same. Among the functional traits I studied, the strongest predictor of species drought survival was leaf mass fraction, whereas the strongest predictor of species position on the rainfall gradient (species mean annual rainfall minimum) was SLA. In addition, plasticity in LMF was positively related to drought survival in the greenhouse (Chapter 3, Fig. 3b). LMF and SLA are related to biomass allocation to leaves and morphology of plants. As morphological and biomass allocation traits can easily be measured, they are good candidate traits for predicting species drought survival and position on the rainfall gradient.

In summary, this study identified two plant drought adaptation strategy axes: (1) dense tissues and physiological drought tolerance versus drought avoidance and height expansion and (2) resource acquisition versus resource conservation (Chapter 4, Fig.1). Fast-growing species mostly exhibited a *drought avoidance* (deciduousness) strategy, whereas shade-tolerant and non- pioneer light-demanding species with high tissue density exhibited a *physiological drought tolerance* strategy. The results of the study suggest that tolerance to drought is associated with shade tolerance and slow growth rate. It must be noted here that in the greenhouse we found interaction between light and water in 40% of the traits studied, including RGR. It is likely these traits may to some extent contribute to the association between physiological drought tolerance and shade tolerance mentioned here (Chapter 4, Fig. 1). In the drought experiment in the greenhouse (Chapter 3, Table 1) nine out of the ten species that survived nine weeks of experimental drought are non-pioneer light demanders and shade-tolerant species and may be using the strategy of physiological drought tolerance.

4. Plant performance and it relationship with species distribution (Q4)

Species distribution along a rainfall gradient is thought to be shaped by drought, shade, soil fertility, pests and pathogens (Chapter 1, Fig. 1). Species drought performance (growth and survival) in the dry forest relative to the wet forest correlated negatively with species rainfall minimum and optimum (Fig. 6.3d, Chapter 5, Fig. 7). It can therefore be inferred that the species that performed relatively well in dry forest or under dry conditions tend to occur in drier forests (cf. Engelbrecht *et al.* 2007, Poorter & Markesteijn 2008, Baltzer *et al.* 2008, Sterck *et al.* 2014). My results show that seasonal drought plays an important role in tree species distribution, but as a large part of the variation remains unexplained, other non-climatic factors (biotic and disturbance regimes) must also shape a species' distribution.

Low SLA is associated with wet forest species (Fig 6.3c) and may be a strategy to avoid herbivore attack, or an adaptation to the shaded conditions of wet forest, where low SLA enhances leaf longevity, in the shaded understory.

Soil fertility differs between dry and wet forest along the rainfall gradient and studies have found an association between soil nutrients and species distribution (Swaine 1996, Condit *et al.* 2013). Yet a greenhouse (20% irradiance) drought experiment with soils from wet and dry forests and 18 of 24 tree species used in this study, showed no significant difference in survival between species growing on wet-forest soil and dry-forest soil at the end of 8 weeks. Over a period of 12 weeks in the greenhouse (20% irradiance), species growing on the dry-forest soil and watered daily performed better (higher RGR, Fig 6.3b) than species growing on the wet-forest soil and watered daily. Furthermore, only few species responded significantly in terms of growth to these soil differences and there was no significant interaction between soil type and species on the RGR of species growing in both the wet treatment and the dry treatment (L. Amissah *et al.* unpublished data). Similar results were obtained by Veenendaal *et al.* (1996c).

Pest pressure (insect herbivory rate) differs significantly along the rainfall gradient (Coley & Barone 1996) and may influence the distribution of species. Insect herbivory rates were evaluated for two months on the 23 species planted in the reciprocal planting experiment reported in Chapter 5. The study showed that herbivory rates were higher in dry forest than in the wet forest (Fig. 6.3a). This suggests that, contrary to expectation, herbivore pressure is higher in the dry forest than in the wet forest, or that in the dry forest the leaves are less well protected. The study showed significant interaction effects of forest type and species distribution. However, dry forest species showed no home advantage (i.e. were not able to perform better in their natural habitat than a species from another habitat, when these two species were grown together). They suffered more herbivory in the dry forest than in the wet forest, from which it can be concluded

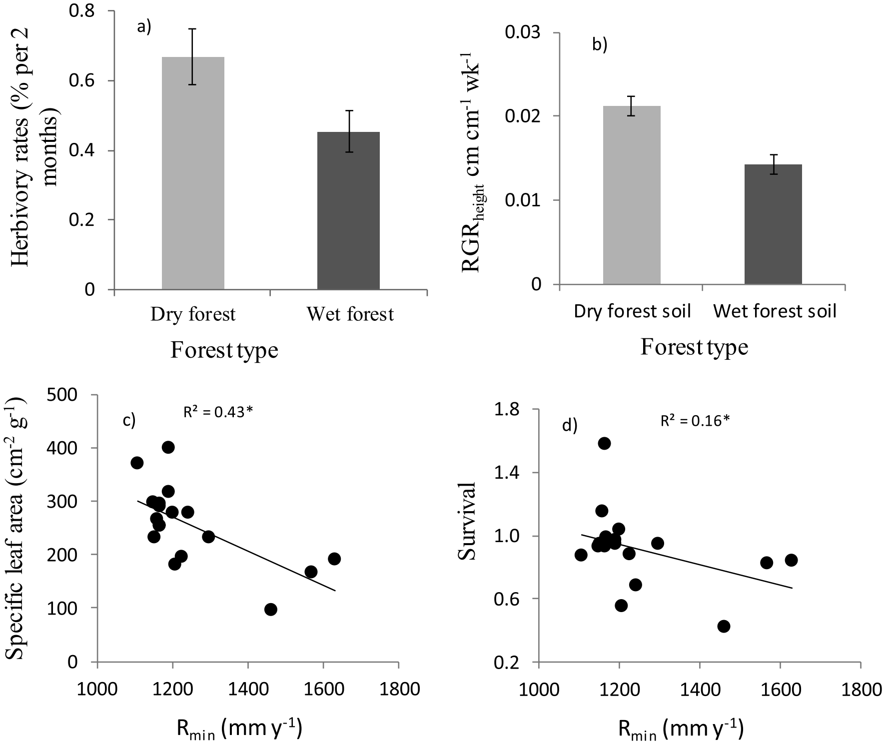


Figure 6.3. Overview of potential role of different environmental factors (pests, soil fertility, shade, drought) in the performance and distribution of Ghanaian tree species along the rainfall gradient. (a) pest pressure; herbivory rates of saplings in dry and wet forest, (b) soil fertility; the effect of fertile soil from dry forest and infertile soil from wet forest on the relative height growth rate of seedlings in a greenhouse experiment, (c) shade; adaptation to forest shade that increases along the rainfall gradient. High rainfall species have a low specific leaf area (Chapter 4); and (d) drought survival (quantified as the survival in the dry forest relative to survival in the wet forest, Chapter 5). For panel (a), data came from measuring rate of herbivory on ten saplings per species for 23 species planted in a reciprocal planting experiment in wet forest (Neung South Forest Reserve) and in dry forest (Afram Headwaters Forest Reserve). Herbivory rates were measured on two leaves per sapling for two months by S. Sportel and L. Amissah (data not included in this thesis). For panel (b), data came from a greenhouse (20% full sunlight) experiment with 18 of the study species using 12 replicates per species (six individuals on soils from wet forest and six individuals on soil from dry forest). Plants were grown for a period of 12 weeks and watered daily, and plant height was measured every two weeks. Relative height growth rate was calculated from height at initial census and height at 12 weeks (L. Amissah *et al.* unpublished data). For panels (c) and (d) each dot represents a species; in total there were 18 species.

that water availability and shade play a much stronger role in species distribution than do soil and herbivores (Fig. 6.2). In the 2-year field reciprocal transplantation experiment (Chapter 5) dry forest species showed home advantage compared to wet forest species; their growth in dry forest were better. By contrast, the wet forest species did not enjoy any home advantage. Hence, the explanation for the success of dry forest species in dry habitats is their drought tolerance, and it is the lack of drought tolerance that explains why wet forest species do not occur in seasonally dry areas. It is not clear, however, what excludes dry species from wet forest, as in Chapter 5 Fig. 5, I showed that in wet forest gaps, the dry species grow even better than the wet species. May be this counterintuitive result can be explained by the light-demanding nature of many dry forest species. If the experiment had been carried out in the shaded understory, then these light-demanding dry forest species might have lost out to the wet forest species. The few deciduous dry forest species included in this study might find it difficult to replace shed leaves, because in the shaded understory carbon gain is low. And the evergreen dry forest species may have dense stems, which enhance their physiological drought tolerance but might also retard height growth. The wet species included in this study were mostly non-pioneer light demanders and shade tolerant, and it is possible that growing them in a forest gap of 20% full sunlight could have put them at a disadvantage. However, this seems unlikely, because in the greenhouse experiment some of the wet forest species did not survive the nine-week drought under 5% sunlight. Similarly, Baltzer & Davies (2012) found no evidence for a general home advantage for “wet” and “dry” forest species in Southeast Asia. However, in contrast to my study, they did find a home advantage for wet forest species in the wet forest.

Implications for forest ecology, forest management and climate change adaptation

Over the past four decades (1960-1998), annual rainfall in the West Africa tropical forest biome has decreased at a rate of 4% per decade, which is faster than the decrease observed for any other tropical forest region (Malhi & Wright 2004); this trend has been predicted to continue in the near future (Allison *et al*. 2009, Lewis *et al*. 2011). Concomitantly, the frequency and intensity of drought in West Africa has also increased in recent times, and it is expected that seasonal patterns of rainfall and drought will become more important in shaping forests rather than the total quantity of precipitation (Condit 1998, Nepstad *et al*. 2004). These developments will have major consequences for the regeneration phase of tree species and thus for the maintenance of the species composition, diversity and community structure of forest vegetation (Allen *et al*. 2010, Condit *et al*. 1995).

The main effects of global climate change predicted for the tropics are changes in rainfall patterns and more frequent El Niño events (Hulme and Viner

1998; Timmermann *et al.* 1999). This study has shown that the two main climatic drivers influencing tree species distribution in Ghana are annual amount of rainfall and rainfall seasonality (Chapter 2, see also Bongers *et al.* 1999, Condit 1998, Condit *et al.* 2013, Toledo *et al.* 2012, Veenendaal & Swaine 1998). Consequently, a reduction in rainfall, more pronounced seasonality and more frequent drought will constrain tree species establishment, especially in the regenerative phase. Over the last twenty years, dry season rainfall has decreased by about 23% in most forest types in Ghana (Fauset *et al.* 2012). The significant impact of drought on survival and growth that I found in this study shows that locally, drought tolerance is an important selective agent which influences the recruitment patterns and the dynamics of wet and dry forests in Ghana. It is likely that this phenomenon occurs elsewhere in the tropics (cf. Engelbrecht & Kusar 2003). Recruitment of species that are more resistant to drought may not be affected by the normal dry season in the forest of Ghana but may be affected by future increases in dry season intensity and duration. Species field drought survival (i.e. quantified as survival in dry forest relative to wet forest) was found to be related to their position along the rainfall gradient. The results of this study suggest that the ability to resist drought in combination with spatial and temporary differences in soil moisture availability will play a major role in maintenance of diversity and distribution patterns of species in the tropical forest of Ghana. Other factors such as soil nutrients, herbivores and disturbances such as fire (which are mostly associated with drying climate) may act in concert to shape the future distribution of some species.

Many of the study species showed low to intermediate performance under drought (i.e. had no survivors or less than 50% survival in the greenhouse but more than 50% survival in the field, Table 6.3). A number of them (e.g. *Antiaris toxicaria, Terminalia superba, Terminalia ivorensis, Mansonia altissima,* and *Khaya ivorensis*) are currently used in small-scale and large-scale plantation and rehabilitation schemes, but because they fall into the low and intermediate categories they may not survive more intense and frequent drought (Table 6.3). The findings of this study demonstrate the need to use drought tolerance as a criterion for selecting tree species for specific reforestation sites (Craven *et al.* 2011). Matching species to the environment for which they are currently optimally adapted can facilitate plantation survival and growth (Hamann & Wang, 2006) under current and anticipated future climate. Table 6.3 indicates the species with high drought tolerance and those with low drought tolerance, as revealed by the greenhouse and field experiments in this study. The drought tolerance of species that were not included in my study can be screened by examining easy to measure drought tolerance traits, such as deciduousness for the drought avoiders (Table 6.4), or leaf dry matter content for the physiologically drought-tolerant species (Table 6.2, 6.4).

Table 6.2 Traits that predict drought survival in the greenhouse and species distribution.
+ = significant positive relation, - = significant negative relation, o = not a significant relation, ne = not estimated, SLA = Specific leaf area, LAR = leaf area ratio, LMF = leaf mass fraction, LDMC = leaf dry matter content, RDMC = root dry matter content, SD = stem density, SRL= specific root length, RLLA= root length per unit leaf area, LWP_{nd} = leaf water potential at nearly dead stage (moribund), LWP_{sw} = leaf water potential at slightly wilted stage.

Predictors	Drought survival shade house	Drought survival field	Species distribution
SLA	o	ne	-
LAR	-	ne	-
LMF	-	ne	-
LDMC	+	ne	-
RDMC	-	ne	+
SD	+	ne	o
SRL	o	ne	+
RLLA	o	ne	+
LWP_{nd}	o	ne	-
LWP_{sw}	o	ne	-

Other ways to conserve species that are likely to be affected should include conservation of species in gene banks, establishment of ex situ conservation areas, especially in areas that currently experience high rainfall, and the establishment of forest corridors along the gradient, to facilitate the migration of species. Additionally, because the prediction of future rainfall is equivocal, especially for the West Africa climate (i.e. some models predict an increase in rainfall, whereas others predict a decrease), mixed plantations of species with different capacity for drought adaptation should be planted in all ecological zones. Tree improvement programmes should focus on improving the drought-tolerant traits of species used especially for forest restoration and plantation programmes. Current developments in biotechnology and molecular markers may offer a good opportunity to identify quantitative trait loci which control the drought tolerance traits of plants (Guimarães *et al* 2007, Merewitz *et al.* 2012). The drought tolerance traits that could best be genetically mapped are LDMC, RDMC, LMF and LAR, because they are good predictors of drought survival, and species distribution along the rainfall gradient (Table 6.2). This may aid in the selection of appropriate material for plant breeding programmes, which in the past has mostly relied on the phenotypic characteristics of individuals. Finally, corridors need to be created between fragmented forest areas in Ghana, to allow for potential species shifts in response to global climate change (cf. Hawthorne & Abu-Juam 1985, Wieringa & Poorter 2004)

Table 6.3. Species name, ecological guild, and their drought tolerance in the greenhouse (Chapter 3) and the field (Chapter 5). NPLD = non-pioneer light demander, SB = shade tolerant. Low drought tolerance = species are highly sensitive to drought in both the greenhouse and in the field (i.e. species had no survivors in the 20% greenhouse but more than 50% survival in the field); intermediate drought tolerance = species showing low survival (less than or equal to 50%) in the greenhouse but high (more than 50%) survival in the field; High drought tolerance = species showing high survival (more than 50%) to drought both in the greenhouse and the field.

Species name	Species guild	Drought tolerance
Albizia zygia	NPLD	high
**Aningeria robusta (Pouteria aningeri)*	NPLD	
Ceiba pentandra	Pioneer	high
Entandrophragma angolense	NPLD	high
Pericopsis elata	NPLD	high
Piptadeniastrum africanum	NPLD	high
Antiaris toxicaria	NPLD	intermediate
Celtis zenkeri	NPLD	intermediate
Newbouldia laevis	Pioneer	intermediate
Ricinodendron heudelotii	Pioneer	intermediate
Strombosis pustulata	SB	intermediate
Sterculia rhinopetala	NPLD	high
Turraeanthus africanus	SB	intermediate
Heritiera utilis	NPLD	low
Khaya anthotheca	NPLD	low
Khaya ivorensis	NPLD	low
Lophira alata	Pioneer	low
Mansonia altissima	NPLD	low
Nesogordonia papaverifera	SB	low
Pentadesma butyracea	SB	low
Terminalia ivorensis$_{wet}$	Pioneer	low
Terminalia ivorensis$_{dry}$	Pioneer	low
Terminalia superba	Pioneer	low
Tieghemella heckelii	NPLD	low

*Species not included in reciprocal transplanting experiment in the field

Table 6.4 Drought strategies of tropical tree species of Ghana, and their observed association with shade tolerance and species traits. These observed drought strategies was based on 18 traits calculated over seedlings of 24 species that were grown in 20% sunlight greenhouse and watered daily. Traits values were calculated on 16 individuals per species. Drought strategies were identified through a principal component analysis with size corrected mean values of 18 traits and relative growth rate of seedlings. Seedling phenology at the seedling and sapling stage was observed both in the greenhouse and in the field. Species guild follows Hawthorne (1995). NPLD = non-pioneer light demander, SB = shade tolerant, LMF = leaf mass fraction, RMF = root mass fraction, LDMC = leaf dry matter content, SD = stem density, SLA= specific leaf area, LAR = leaf area ratio, LWP = leaf water potential.

Species guild and traits	Drought avoidance	Drought delay	Drought tolerance
Shade tolerance guild	Pioneers	NPLD	SB
<u>Phenology</u>	Deciduous	Evergreen	Evergreen
<u>Allocation</u>			
LMF	High	Low	High
RMF	Low	High	High
<u>Tissue density</u>			
LDMC	Low	Intermediate	High
SD	Low	Intermediate	High
SLA	High	Intermediate	Low
LAR	High	Intermediate	Low
<u>Physiology</u>			
LWP	High (less negative)	Intermediate	Low (more negative)

CONCLUSIONS

Rainfall and rainfall seasonality explained most of the variation in species distribution in Ghana, in agreement with the findings of several other studies, whereas temperature was found to affect the distribution of certain species only. There is a trade-off between drought avoidance strategy and drought tolerance strategy and this is closely associated with a species' regeneration requirements and growth rates (Table 6.4). Functional traits that predict drought survival and species position on the rainfall gradient are mostly related to allocation (low LMF), morphology (low LAR) and tissue density (high LDMC). Therefore, in the absence of resources to measure physiological traits, morphological traits can be used to predict species drought survival and distribution on the rainfall gradient. Low water availability preclude wet forest species from occurring in dry forest, but low soil nutrients may not be the factor that excludes dry forest species from wet forest. In summary, what shapes species distribution along the rainfall gradient is water availability in particular and, to a lesser extent, shade tolerance, and these are stronger drivers of species distribution along the rainfall gradient than soil nutrients and pests (Fig 6.1).

References

Ackerly D. (2004). Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. *Ecological Monographs,* 74, 25-44.

Ackerly D., Knight C., Weiss S., Barton K. & Starmer K. (2002). Leaf size, specific leaf area and microhabitat distribution of chaparral woody plants: contrasting patterns in species level and community level analyses. *Oecologia* 130, 449-457.

Aerts R. (1999). Interspecific competition in natural plant communities: mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*, 50, 29-37.

Ågren J. & Schemske D.W. (2012). Reciprocal transplants demonstrate strong adaptive differentiation of the model organism Arabidopsis thaliana in its native range. *New Phytologist,* 194, 1112-1122.

Agyeman V., Swaine M. & Thompson J. (1999). Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*, 87, 815-827.

Ahn P.M. (1970). *West African Soils*. Oxford University Press, Oxford.

Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D. & Hogg E. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* 259, 660-684.

Allison I., Bindoff N., Bindschadler R., Cox P., de Noblet N., England M., Francis J., Gruber N., Haywood A. & Karoly D. (2011). The Copenhagen Diagnosis: Updating the world on the latest climate science.

Amissah L., Mohren, G.M.J., Bongers, F., Hawthorne, W.D., Poorter, L. Rainfall and temperature affect tree species distribution in Ghana, *Journal of Tropical Ecology* in press

Aranda I., Castro L., Pardos M., Gil L. & Pardos J.A. (2005). Effects of the interaction between drought and shade on water relations, gas exchange and morphological traits in cork oak (Quercus suber L.) seedlings. *Forest Ecology and Management,* 210, 117-129.

Augspurger C.K. & Kelly C.K. (1984). Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. *Oecologia,* 61, 211-217.

Austin M. & Smith T. (1990). A new model for the continuum concept. In: *Progress in theoretical vegetation science*. Springer, pp. 35-47.

Baker T.R., Burslem D. & Swaine M.D. (2003). Associations between tree growth, soil fertility and water availability at local and regional scales in Ghanaian tropical rain forest. *Journal of Tropical Ecology*, 19, 109-125.

Baltzer J.L. & Davies S.J. (2012). Rainfall seasonality and pest pressure as determinants of tropical tree species' distributions. *Ecology and evolution*, 2, 2682-94.

Baltzer J.L., Davies S.J., Bunyavejchewin S. & Noor N. (2008). The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. *Functional Ecology*, 22, 221-231.

Baltzer J.L. & Thomas S.C. (2010). A second dimension to the leaf economics spectrum predicts edaphic habitat association in a tropical forest. *PloS one*, 5.

Baraloto C., Goldberg D.E. & Bonal D. (2005). Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology*, 86, 2461-2472.

Becker P., Rabenold P.E., Idol J.R. & Smith A.P. (1988). Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology*, 4, 173-184.

Becker P. & Wong M. (1993). Drought-induced mortality in tropical heath forest. *Journal of Tropical Forest Science*, 5, 416-419.

Beer C., Reichstein M., Tomelleri E., Ciais P., Jung M., Carvalhais N., Rödenbeck C., Arain M.A., Baldocchi D., Bonan G.B., Bondeau A., Cescatti A., Lasslop G., Lindroth A., Lomas M., Luyssaert S., Margolis H., Oleson K.W., Roupsard O., Veenendaal E., Viovy N., Williams C., Woodward F.I. & Papale D. (2010). Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, 329, 834-838.

Bongers F., Poorter L., Rompaey R. & Parren M. (1999). Distribution of twelve moist forest canopy tree species in Liberia and Cote d'Ivoire: response curves to a climatic gradient. *Journal of Vegetation Science*, 10, 371-382.

Borchert R. (1998). Responses of tropical trees to rainfall seasonality and its long-term changes. In: *Potential Impacts of Climate Change on Tropical Forest Ecosystems*. Springer, pp. 241-253.

Boyer J.S. (1982). Plant productivity and environment. *Science*, 218, 443-448.

Brando P.M., Nepstad D.C., Davidson E.A., Trumbore S.E., Ray D. & Camargo P. (2008). Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 1839-1848.

Brenes-Arguedas T., Coley P.D. & Kursar T.A. (2009). Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology*, 90, 1751-1761.

Brenes-Arguedas T., Rios M., Rivas-Torres G., Blundo C., Coley P.D. & Kursar T.A. (2008). The effect of soil on the growth performance of tropical species with contrasting distributions. *Oikos*, 117, 1453-1460.

Brenes-Arguedas T., Roddy A.B., Coley P.D. & Kursar T.A. (2011). Do differences in understory light contribute to species distributions along a tropical rainfall gradient? *Oecologia*, 166, 443-56.

Brenes-Arguedas T., Roddy A.B., Kursar T.A. & Tjoelker M. (2013). Plant traits in relation to the performance and distribution of woody species in wet and dry tropical forest types in Panama. *Functional Ecology*, 27, 392-402.

Brodribb T.J., Bowman D.J., Nichols S., Delzon S. & Burlett R. (2010). Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytologist*, 188, 533-542.

Brodribb T.J. & Cochard H. (2009). Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant physiology*, 149, 575-84.

Brouwer R. (963).Some aspects of the equilibrium between overground and underground plant parts. *Jaarboek van het Instituut voor Biologisch en Scheikundig onderzoek aan Landbouwgewassen* 213: 31–39.

Bullock S.H., Mooney H.A. & Medina E. (1995). *Seasonally dry tropical forests*. Cambridge University Press.

Burslem D.F.R.P., Grubb P.J. & Turner I.M. (1996). Responses to Simulated Drought and Elevated Nutrient Supply among Shade-Tolerant Tree Seedlings of Lowland Tropical Forest in Singapore. *Biotropica*, 28, 636-648.

Cao K.-F. (2000). Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *Journal of Tropical Ecology*, 16, 101-116.

Carter E., Theodorou M. & Morris P. (1997). Responses of Lotus corniculatus to environmental change. *New Phytologist*, 136, 245-253.

Chapin III S., F, Autumn K. & Pugnaire F. (1993). Evolution of suites of traits in response to environmental stress. *The American Naturalist*, 142, S78-S92.

Chaturvedi R.K., Raghubanshi A.S. & Singh J.S. (2012). Growth of tree seedlings in a tropical dry forest in relation to soil moisture and leaf traits. *Journal of Plant Ecology*, 6, 158-170.

Chave J., Coomes D., Jansen S., Lewis S.L., Swenson N.G. & Zanne A.E. (2009). Towards a worldwide wood economics spectrum. *Ecology letters*, 12, 351-366.

Choat B., Ball M.C., Luly J.G., Donnelly C.F. & Holtum J.A. (2006). Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology. *Tree physiology*, 26, 657-664.

Choat B., Jansen S., Brodribb T.J., Cochard H., Delzon S., Bhaskar R., Bucci S.J., Feild T.S., Gleason S.M., Hacke U.G., Jacobsen A.L., Lens F., Maherali H., Martinez-Vilalta J., Mayr S., Mencuccini M., Mitchell P.J., Nardini A., Pittermann J., Pratt R.B., Sperry J.S., Westoby M., Wright I.J. & Zanne A.E. (2012). Global convergence in the vulnerability of forests to drought. *Nature*, 491, 752-5.

Clark D.A., Piper S., Keeling C. & Clark D. (2003). Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences*, 100, 5852-5857.

Clark D.B., Clark D.A. & Oberbauer S.F. (2010). Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO2. *Global Change Biology*, 16, 747-759.

Coley P.D. (1998). Possible effects of climate change on plant/herbivore interactions in moist tropical forests. In: *Potential Impacts of Climate Change on Tropical Forest Ecosystems*. Springer, pp. 315-332.

Coley P.D. & Barone J. (1996). Herbivory and plant defenses in tropical forests. *Annual review of ecology and systematics*, 27, 305-335.

Comita L.S. & Engelbrecht B.M. (2009). Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology*, 90, 2755-2765.

Condit R. (1998). Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change*, 39, 413-427.

Condit R., Engelbrecht B.M., Pino D., Pérez R. & Turner B.L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proceedings of the National Academy of Sciences*, 110, 5064-5068.

Condit R., Hubbell S.P. & Foster R.B. (1995). Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological monographs*, 65, 419-439.

Connell J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations*, 298, 298-312.

Corlett R.T. (2011). Impacts of warming on tropical lowland rainforests. *Trends in ecology & evolution*, 26, 606-13.

Costa M.H., Biajoli M.C., Sanches L., Malhado A.C.M., Hutyra L.R., da Rocha H.R., Aguiar R.G. & de Araújo A.C. (2010). Atmospheric versus vegetation controls of Amazonian tropical rain forest evapotranspiration: Are the wet and seasonally dry rain forests any different? *Journal of Geophysical Research*, 115.

Cox P.M., Harris P.P., Huntingford C., Betts R.A., Collins M., Jones C.D., Jupp T.E., Marengo J.A. & Nobre C.A. (2008). Increasing risk of Amazonian drought due to decreasing aerosol pollution. *Nature*, 453, 212-215.

Craven D., Dent D., Braden D., Ashton M.S., Berlyn G.P. & Hall J.S. (2011). Seasonal variability of photosynthetic characteristics influences growth of eight tropical tree species at two sites with contrasting precipitation in Panama. *Forest Ecology and Management*, 261, 1643-1653.

Currie D.J. & Paquin V. (1987). Large-scale biogeographical patterns of species richness of trees. *Nature*, 329, 326-327.

Davidar P., Puyravaud J.P. & Leigh E.G. (2005). Changes in rain forest tree diversity, dominance and rarity across a seasonality gradient in the Western Ghats, India. *Journal of Biogeography*, 32, 493-501.

Davidar P., Rajagopal B., Mohandass D., Puyravaud J.-P., Condit R., Wright S.J. & Leigh E.G. (2007). The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography*, 16, 510-518.

Davies S.J., Tan S., LaFrankie J.V. & Potts M.D. (2005). Soil-related floristic variation in a hyperdiverse dipterocarp forest. In: *Pollination Ecology and the Rain Forest*. Springer, pp. 22-34.

Deines J.M., Hellmann J.J. & Curran T.J. (2011). Traits associated with drought survival in three Australian tropical rainforest seedlings. *Australian Journal of Botany*, 59, 621.

Deka R., Wairiu M., Mtakwa P., Mullins C., Veenendaal E. & Townend J. (1995). Use and accuracy of the filter-paper technique for measurement of soil matric potential. *European Journal of Soil Science*, 46, 233-238.

Diaz S., Hodgson J., Thompson K., Cabido M., Cornelissen J., Jalili A., Montserrat-Marti G., Grime J., Zarrinkamar F. & Asri Y. (2004a). The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, 15, 295-304.

Diaz S., Hodgson J., Thompson K., Cabido M., Cornelissen J., Jalili A., Montserrat-Marti G., Grime J., Zarrinkamar F., Asri Y., Band S.R., Basconcelo S., Castro-Díez P., Funes G., Hamzehee B., Khoshnevi M., Pérez-Harguindeguy N., Pérez-Rontomé M.C., Shirvany F.A., Vendramini F., Yazdani S., Abbas-Azimi R., Bogaard A., Boustani, S., , Charles M., Dehghan M., de Torres-Espuny L., Falczuk V., Guerrero-Campo J., Hynd A., Jones G., Kowsary E., Kazemi-Saeed F., Maestro-Martínez M., Romo-Díez A., Shaw S., Siavash B., Villar-Salvador P. & and Zak M.R. (2004b). The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, 15, 295-304.

Doughty C.E. & Goulden M.L. (2008). Are tropical forests near a high temperature threshold? *Journal of Geophysical Research: Biogeosciences (2005–2012)*, 113.

Duclos V., Boudreau S. & Chapman C.A. (2013). Shrub Cover Influence on Seedling Growth and Survival Following Logging of a Tropical Forest. *Biotropica*, 45, 419-426.

Duff G., Myers B., Williams R., Eamus D., O'Grady A. & Fordyce I. (1997). Seasonal patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn water potential in a northern Australian savanna. *Australian Journal of Botany*, 45, 211-224.

Duncan R.P., Cassey P. & Blackburn T.M. (2009). Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proceedings. Biological sciences / The Royal Society*, 276, 1449-57.

Engelbrecht B.M., Comita L.S., Condit R., Kursar T.A., Tyree M.T., Turner B.L. & Hubbell S.P. (2007a). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447, 80-2.

Engelbrecht B.M., Dalling J.W., Pearson T.R., Wolf R.L., Galvez D.A., Koehler T., Tyree M.T. & Kursar T.A. (2006). Short dry spells in the wet season increase mortality of tropical pioneer seedlings. *Oecologia*, 148, 258-69.

Engelbrecht B.M. & Kursar T.A. (2003). Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, 136, 383-93.

Engelbrecht B.M.J., Kursar T.A. & Tyree M.T. (2005). Drought effects on seedling survival in a tropical moist forest. *Trees*, 19, 312-321.

Engelbrecht B.M.J., Tyree M.T. & Kursar T.A. (2007b). Visual assessment of wilting as a measure of leaf water potential and seedling drought survival. *Journal of Tropical Ecology*, 23, 497.

Engelbrecht B.M.J., Wright S.J. & De Steven D. (2002). Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical Ecology*, 18.

Erice G., Louahlia S., Irigoyen J.J., Sanchez-Diaz M. & Avice J.C. (2010). Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. *Journal of plant physiology*, 167, 114-20.

Evans J. & Poorter H. (2001). Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell & Environment*, 24, 755-767.

Fauset S., Baker T.R., Lewis S.L., Feldpausch T.R., Affum-Baffoe K., Foli E.G., Hamer K.C. & Swaine M.D. (2012). Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana. *Ecology letters*, 15, 1120-9.

Fayolle A., Engelbrecht B., Freycon V., Mortier F., Swaine M., Rejou-Mechain M., Doucet J.L., Fauvet N., Cornu G. & Gourlet-Fleury S. (2012). Geological substrates shape tree species and trait distributions in African moist forests. *PloS one*, 7, e42381.

Feeley K.J., Wright S.J., Nur Supardi M.N., Kassim A.R. & Davies S.J. (2007). Decelerating growth in tropical forest trees. *Ecology letters*, 10, 461-469.

Fisher B.L., Howe H.F. & Wright S.J. (1991). Survival and growth of Virola surinamensis yearlings: water augmentation in gap and understory. *Oecologia*, 86, 292-297.

Fonseca C.R., Overton J.M., Collins B. & Westoby M. (2000). Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, 88, 964-977.

Galbraith D., Levy P.E., Sitch S., Huntingford C., Cox P., Williams M. & Meir P. (2010). Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *New Phytologist*, 187, 647-665.

Garwood N.C. (1996). Functional morphology of tropical tree seedlings. *MAN AND THE BIOSPHERE SERIES*, 17, 59-130.

Gauch Jr H. & Whittaker R. (1972). Coenocline simulation. *Ecology*, 53, 446-451.

Gentry A.H. (1988). Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden (USA)*.

Gerhardt K. (1993). Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *Journal of Vegetation Science*, 4, 95-102.

Gerhardt K. (1996). Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, 82, 33-48.

Givnish T.J. (1988). Adaptation to sun and shade: a whole-plant perspective. *Functional Plant Biology*, 15, 63-92.

Givnish T.J. (2002). Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica*, 36, 703-743.

Gommers C.M., Visser E.J., Onge K.R.S., Voesenek L.A. & Pierik R. (2013). Shade tolerance: when growing tall is not an option. *Trends in plant science*, 18, 65-71.

Government of Ghana. (2011). *Ghana's second national communication to UNFCC*. Environmental Protection Agency, Accra.168 pp.

Goulden M.L., Miller S.D., Da Rocha H.R., Menton M.C., de Freitas H.C., e Silva Figueira A.M. & de Sousa C.A.D. (2004). Diel and seasonal patterns of tropical forest CO2 exchange. *Ecological Applications*, 14, 42-54.

Grime J., Thompson K., Hunt R., Hodgson J., Cornelissen J., Rorison I., Hendry G., Ashenden T., Askew A., Band S., R. E. Booth, C. C. Bossard, B. D. Campbell, J. E. L. Cooper A.W.D., P. L. Gupta, W. Hall, D. W. Hand, M. A. Hannah, S. H. Hillier, D. J. Hodkinson, A. Jalili, Z. Liu, J. M. L. Mackey, N. Matthews, M. A. Mowforth, A. M. Neal, R. J. Reader, K. Reiling, W. Ross-Fraser, R. E. Spencer, F. Sutton, D. E. Tasker, Thorpe P.C. & Whitehouse a.J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos*, 259-281.

Grubb P.J. (1998). A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics*, 1, 3-31.

Guimarães E.P. (2007). *Marker-assisted selection: current status and future perspectives in crops, livestock, forestry and fish*. Food & Agriculture Org.

Hacke U.G., Sperry J.S., Pockman W.T., Davis S.D. & McCulloh K.A. (2001). Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia,* 126, 457-461.

Hacke U.G., Sperry J.S., Wheeler J.K. & Castro L. (2006). Scaling of angiosperm xylem structure with safety and efficiency. *Tree physiology,* 26, 689-701.

Hall J. & Swaine M.D. (1976). Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology,* 64, 913-951.

Hall J.B. & Swaine M.D. (1981). *Distribution and ecology of vascular plants in a tropical rain forest. Forest vegetation in Ghana*. Dr W. Junk Publishers.

Hamann A. & Wang T. (2006). Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology,* 87, 2773-2786.

Hawthorne, W.D. (1995) *Ecological profiles of Ghanaian forest trees. Tropical Forestry Paper* 29, Oxford Forestry Institute, Oxford. 345 pp.

Hawthorne, W.D. & Abu-Juam, M. (1995) *Forest protection in Ghana*. IUCN, Gland and Cambridge. 219 pp.

Hawthorne, W. D. & Gyakari, N. (2006) *Photo guide for the forest trees of Ghana. A tree-spotter's field guide for identifying largest trees*. Oxford Forestry Institute, Oxford. 432 pp.

Hawthorne, W. D & Jongkind, C. (2006) *Woody plants of western African forests. A guide to the forest trees, shrubs and lianas from Senegal to Ghana*. Royal Botanic Gardens, Kew.1040 pp.

Hawthorne W.D. (1996). Holes and the sums of parts in Ghanaian forest: regeneration, scale and sustainable use. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences,* 104, 75-176.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* 25, 1965-1978.

Hoffmann W.A. & Poorter H. (2002). Avoiding bias in calculations of relative growth rate. *Annals of botany,* 90, 37-42.

Holbrook N.M., Whitbeck J.L. & Mooney H.A. (1995). Drought responses of neotropical dry forest trees. *Seasonally dry tropical forests. Cambridge University Press, Cambridge,* 243-276.

Holmgren M. & Poorter L. (2007). Does a ruderal strategy dominate the endemic flora of the West African forests? *Journal of Biogeography,* 34, 1100-1111.

Holmgren M., Poorter L. & Siepel A. (2004). What explains the distribution of rare and endemic West African plants? *Biodiversity of West African forests: an ecological atlas of woody plant species,* 73-85.

Holmgren M., Scheffer M. & Huston M.A. (1997). The interplay of facilitation and competition in plant communities. *Ecology*, 78, 1966-1975.

Holmgren M., Segura A.M. & Fuentes E.R. (2000). Limiting mechanisms in the regeneration of the Chilean matorral–Experiments on seedling establishment in burned and cleared mesic sites. *Plant Ecology*, 147, 49-57.

Holste E.K., Kobe R.K. & Vriesendorp C.F. (2011). Seedling growth responses to soil resources in the understory of a wet tropical forest. *Ecology*, 92, 1828-1838.

Hulme M., Doherty R., Ngara T., New M. & Lister D. (2001). African climate change: 1900-2100. *Climate research*, 17, 145-168.

Hulme M. & Viner D. (1998). A climate change scenario for the tropics. In: *Potential Impacts of Climate Change on Tropical Forest Ecosystems*. Springer, pp. 5-36.

Iida Y., Poorter L., Sterck F.J., Kassim A.R., Kubo T., Potts M.D. & Kohyama T.S. (2012). Wood density explains architectural differentiation across 145 co-occurring tropical tree species. *Functional Ecology*, 26, 274-282.

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

Jacobsen A.L., Ewers F.W., Pratt R.B., Paddock W.A. & Davis S.D. (2005). Do xylem fibers affect vessel cavitation resistance? *Plant physiology*, 139, 546-556.

Jacobsen A.L., Pratt R.B., Ewers F.W. & Davis S.D. (2007). Cavitation resistance among 26 chaparral species of southern California. *Ecological Monographs*, 77, 99-115.

Jahns S. (1996). Vegetation history and climate changes in West Equatorial Africa during the Late Pleistocene and Holocene, based on a marine pollen diagram from the Congo fan. *Vegetation History and Archaeobotany*, 5, 207-213.

Janzen D.H. (1967). Why mountain passes are higher in the tropics. *American Naturalist*, 233-249.

John R., Dalling J.W., Harms K.E., Yavitt J.B., Stallard R.F., Mirabello M., Hubbell S.P., Valencia R., Navarrete H., Vallejo M. & Foster R.B. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences*, 104, 864-869.

Johnson J.B. & Omland K.S. (2004). Model selection in ecology and evolution. *Trends in ecology & evolution*, 19, 101-108.

Jongkind C.C.H., Wieringa, J.J. (2004). Checklist of Upper Guinea forest species. In Poorter, L., F. Bongers, F. N.Kouame, W.D. Hawthorne (Eds.). Biodiversity of West African forests: An ecological atlas of woody plant species. CABI Publishing, Wallingford, UK.

Kato M., Itioka T., Sakai S., Momose K., Yamane S., Hamid A.A. & Inoue T. (2000). Various population fluctuation patterns of light-attracted beetles in a tropical lowland dipterocarp forest in Sarawak. *Population Ecology,* 42, 97-104.

Kitajima K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia,* 98, 419-428.

Kitajima K. & Poorter L. (2010). Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *The New phytologist,* 186, 708-21.

Kraft N.J., Valencia R. & Ackerly D.D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science,* 322, 580-2.

Kröber W., Böhnke M., Welk E., Wirth C. & Bruelheide H. (2012). Leaf trait-environment relationships in a subtropical broadleaved forest in south-east China. *PloS one,* 7, e35742.

Kursar T.A., Engelbrecht B.M.J., Burke A., Tyree M.T., Ei Omari B. & Giraldo J.P. (2009). Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology,* 23, 93-102.

Kyereh B., Swaine M. & Thompson J. (1999). Effect of light on the germination of forest trees in Ghana. *Journal of Ecology,* 87, 772-783.

Lawesson J.E. & Oksanen J. (2002). Niche characteristics of Danish woody species as derived from coenoclines. *Journal of Vegetation Science,* 13, 279-290.

Lebrija-Trejos E., Pérez-García E.A., Meave J.A., Poorter L. & Bongers F. (2011). Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology,* 27, 477-489.

Lens F., Tixier A., Cochard H., Sperry J.S., Jansen S. & Herbette S. (2013). Embolism resistance as a key mechanism to understand adaptive plant strategies. *Current opinion in plant biology,* 16, 287-292.

Levine J.M. & Murrell D.J. (2003). The community-Level consequences Of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics,* 34, 549-574.

Lewis S.L., Brando P.M., Phillips O.L., van der Heijden G.M. & Nepstad D. (2011). The 2010 amazon drought. *Science,* 331, 554-554.

Lewis S.L., Malhi Y. & Phillips O.L. (2004). Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences,* 359, 437-462.

Lloyd J. & Farquhar G.D. (2008). Effects of rising temperatures and [CO2] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 363, 1811-1817.

Loescher H., Oberbauer S., Gholz H. & Clark D. (2003). Environmental controls on net ecosystem-level carbon exchange and productivity in a Central American tropical wet forest. *Global Change Biology*, 9, 396-412.

Logah F.Y., Obuobie E., Ofori, D. & Kankam-Yeboah K. (2013) Analysis of rainfall variability in Ghana. *International Journal of Latest Research in Engineering and Computing* 1,1-8.

Lohbeck M., Poorter L., Lebrija-Trejos E., Martínez-Ramos M., Meave J.A., Paz H., Pérez-García E.A., Romero-Pérez I.E., Tauro A. & Bongers F. (2013). Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, 94, 1211-1216.

Lopez-Iglesias B., Villar R. & Poorter L. (2014). Functional traits predict drought performance and distribution of Mediterranean woody species. *Acta Oecologica*, 56, 10-18.

Maharjan S.K., Poorter L., Holmgren M., Bongers F., Wieringa J.J. & Hawthorne W.D. (2011). Plant functional traits and the distribution of West African rain forest trees along the rainfall gradient. *Biotropica*, 43, 552-561.

Malhi Y., Aragao L.E., Galbraith D., Huntingford C., Fisher R., Zelazowski P., Sitch S., McSweeney C. & Meir P. (2009). Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. *Proceedings of National Academy of Science U S A*, 106, 20610-5.

Malhi Y. & Wright J. (2004). Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 359, 311-329.

Mark P. & Ashton S. (1992). Some measurements of the microclimate within a Sri Lankan tropical rainforest. *Agricultural and Forest Meteorology*, 59, 217-235.

Markesteijn L., Iraipi J., Bongers F. & Poorter L. (2010). Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. *Journal of Tropical Ecology*, 26, 497-508.

Markesteijn L. & Poorter L. (2009). Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology*, 97, 311-325.

Markesteijn L., Poorter L., Paz H., Sack L. & Bongers F. (2011). Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits. *Plant, Cell & Environment*, 34, 137-148.

Marod D., Kutintara U., Tanaka H. & Nakashizuka T. (2002). The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology*, 161, 41-57.

McDowell N., Pockman W.T., Allen C.D., Breshears D.D., Cobb N., Kolb T., Plaut J., Sperry J., West A. & Williams D.G. (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist*, 178, 719-739.

McKenzie D., Peterson D.W., Peterson D.L. & Thornton P.E. (2003). Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. *Journal of Biogeography*, 30, 1093-1108.

Meinzer F.C., Woodruff D.R., Domec J.C., Goldstein G., Campanello P.I., Gatti M.G. & Villalobos-Vega R. (2008). Coordination of leaf and stem water transport properties in tropical forest trees. *Oecologia*, 156, 31-41.

Méndez-Alonzo R., Paz H., Zuluaga R.C., Rosell J.A. & Olson M.E. (2012). Coordinated evolution of leaf and stem economics in tropical dry forest trees. *Ecology*, 93, 2397-2406.

Méndez-Alonzo R., Pineda-García F., Paz H., Rosell J.A. & Olson M.E. (2013). Leaf phenology is associated with soil water availability and xylem traits in a tropical dry forest. *Trees*, 27, 745-754.

Merewitz E.B., Belanger F.C., Warnke S.E. & Huang B. (2012). Identification of Quantitative Trait Loci Linked to Drought Tolerance in a Colonial× Creeping Bentgrass Hybrid Population. *Crop Science*, 52, 1891-1901.

Metz C.E. (1978). Basic principles of ROC analysis. In: *Seminars in nuclear medicine*. Elsevier, pp. 283-298.

Milla R., Reich P., Niinemets Ü. & Castro-Díez P. (2008). Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Functional ecology*, 22, 565-576.

Moles A.T., Warton D.I., Warman L., Swenson N.G., Laffan S.W., Zanne A.E., Pitman A., Hemmings F.A. & Leishman M.R. (2009). Global patterns in plant height. *Journal of Ecology*, 97, 923-932.

Moreno J. & Oechel W. (1992). Factors controlling postfire seedling establishment in southern California chaparral. *Oecologia*, 90, 50-60.

Mulkey S.S., Smith A.P. & Wright S.J. (1991). Comparative life history and physiology of two understory Neotropical herbs. *Oecologia*, 88, 263-273.

Muller-Landau H.C. (2004). Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, 36, 20-32.

Murphy P.G. & Lugo A.E. (1986). Ecology of tropical dry forest. *Annual review of ecology and systematics*, 67-88.

Myers B.A., Duff G., Eamus D., Fordyce I., O'Grady A. & Williams R. (1997). Seasonal variation in water relations of trees of differing leaf phenology in a wet–dry tropical savanna near Darwin, northern Australia. *Australian Journal of Botany*, 45, 225-240.

Neilson R.P. & Drapek R.J. (1998). Potentially complex biosphere responses to transient global warming. *Global change biology,* 4, 505-521.

Nepstad D., Lefebvre P., Lopes da Silva U., Tomasella J., Schlesinger P., Solorzano L., Moutinho P., Ray D. & Guerreira Benito J. (2004). Amazon drought and its implications for forest flammability and tree growth: A basin-wide analysis. *Global Change Biology,* 10, 704-717.

Nepstad D.C., Tohver I.M., Ray D., Moutinho P. & Cardinot G. (2007). Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology,* 88, 2259-2269.

Newman E. (1966). A method of estimating the total length of root in a sample. *Journal of applied Ecology,* 3, 139-145.

Ngomanda A., Jolly D., Bentaleb I., Chepstow-Lusty A., Maley J., Fontugne M., Oslisly R. & Rabenkogo N. (2007). Lowland rainforest response to hydrological changes during the last 1500 years in Gabon, Western Equatorial Africa. *Quaternary research,* 67, 411-425.

Nicotra A.B., Babicka N. & Westoby M. (2002). Seedling Root Anatomy and Morphology: An Examination of Ecological Differentiation with Rainfall Using Phylogenetically Independent Contrasts. *Oecologia,* 130, 136-145.

Niinemets Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology,* 82, 453-469.

Niinemets Ü. & Valladares F. (2006). Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs,* 76, 521-547.

O'brien E.M. (1993). Climatic gradients in woody plant species richness: towards an explanation based on an analysis of southern Africa's woody flora. *Journal of Biogeography,* 20, 181-198.

Oksanen J. & Minchin P.R. (2002). Continuum theory revisited: what shape are species responses along ecological gradients? *Ecological Modelling,* 157, 119-129.

Orians G.H. (2000). Biodiversity and Ecosystem Processes in Tropical Ecosystems. *Revista de Biologia Tropical,* 48, 297-303.

Parolin P., Lucas C., Piedade M.T. & Wittmann F. (2010). Drought responses of flood-tolerant trees in Amazonian floodplains. *Annals of botany,* 105, 129-39.

Pausas J.G. & Austin M.P. (2001). Patterns of plant species richness in relation to different environments: an appraisal. *Journal of Vegetation Science,* 12, 153-166.

Pearce J. & Ferrier S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling,* 133, 225-245.

Phillips O.L., Lewis S.L., Baker T.R., Chao K.J. & Higuchi N. (2008). The changing Amazon forest. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences,* 363, 1819-27.

Phillips O.L., Van der Heijden G., Lewis S.L., López-González G., Aragão L.E., Lloyd J., Malhi Y., Monteagudo A., Almeida S. & Dávila E.A. (2010). Drought–mortality relationships for tropical forests. *New Phytologist,* 187, 631-646.

Phillips O.L., Vargas P.N., Monteagudo A.L., Cruz A.P., Zans M.E.C., Sánchez W.G., Yli-Halla M. & Rose S. (2003). Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology,* 91, 757-775.

Poorter H., Bühler J., van Dusschoten D., Climent J. & Postma J.A. (2012). Pot size matters: a meta-analysis of the effects of rooting volume on plant growth. *Functional Plant Biology,* 39, 839-850.

Poorter H. & Nagel O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: a quantitative review. *Functional Plant Biology,* 27, 1191-1191.

Poorter L. (1999). Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional ecology,* 13, 396-410.

Poorter L. (2009). Leaf traits show different relationships with shade tolerance in moist versus dry tropical forests. *The New phytologist,* 181, 890-900.

Poorter L. & Bongers F. (2006). Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology,* 87, 1733-1743.

Poorter L., Bongers, Frans, Kouame ,F. N., Hawthorne, W.D. (2004). *Biodiversity of West African forests: an ecological atlas of woody plant species*. CABI.

Poorter L. & Hayashida-Oliver Y. (2000). Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology,* 16, 481-498.

Poorter L. & Markesteijn L. (2008). Seedling traits determine drought tolerance of tropical tree species. *Biotropica,* 40, 321-331.

Poorter L. & Rose S.A. (2005). Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. *Oecologia,* 142, 378-387.

Pratt R.B., Jacobsen A.L., Ewers F.W. & Davis S.D. (2007). Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist,* 174, 787-98.

Quero J.L., Sterck F.J., Martinez-Vilalta J. & Villar R. (2011). Water-use strategies of six co-existing Mediterranean woody species during a summer drought. *Oecologia,* 166, 45-57.

Quero J.L., Villar R., Marañón T. & Zamora R. (2006). Interactions of drought and shade effects on seedlings of four Quercus species: physiological and structural leaf responses. *New Phytologist,* 170, 819-834.

Quero J.L., Villar R., Marañón T., Zamora R., Vega D. & Sack L. (2008). Relating leaf photosynthetic rate to whole-plant growth: drought and shade effects on seedlings of four Quercus species. *Functional Plant Biology*, 35, 725-737.

Raich J.W., Rastetter E.B., Melillo J.M., Kicklighter D.W., Steudler P.A., Peterson B.J., Grace A.L., Moore B. & Vorosmarty C.J. (1991). Potential Net Primary Productivity in South America: Application of a Global Model. *Ecological Applications*, 1, 399-429.

Rangel T.F., Diniz-Filho J.A.F. & Bini L.M. (2010). SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, 33, 46-50.

Reich P., Tjoelker M., Walters M., Vanderklein D. & Buschena C. (1998). Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*, 12, 327-338.

Ruiz-Robleto J. & Villar R. (2005). Relative growth rate and biomass allocation in ten woody species with different leaf longevity using phylogenetic independent contrasts (PICs). *Plant Biology*, 7, 484-494.

Rydgren K., Økland R.H. & Økland T. (2003). Species response curves along environmental gradients. A case study from SE Norwegian swamp forests. *Journal of Vegetation Science*, 14, 869-880.

Saatchi S., Asefi-Najafabady S., Malhi Y., Aragão L.E., Anderson L.O., Myneni R.B. & Nemani R. (2013). Persistent effects of a severe drought on Amazonian forest canopy. *Proceedings of the National Academy of Sciences*, 110, 565-570.

Sack L. (2004). Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos*, 107, 110-127.

Sack L. & Grubb P.J. (2002). The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. *Oecologia*, 131, 175-185.

Sack L., Grubb P.J. & Marañón T. (2003). The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. *Plant Ecology*, 168, 139-163.

Saldaña A., Gianoli E. & Lusk C. (2005). Ecophysiological responses to light availability in three Blechnum species (Pteridophyta, Blechnaceae) of different ecological breadth. *Oecologia*, 145, 251-256.

Sánchez-Gómez D., Valladares F. & Zavala M.A. (2006). Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. *New Phytologist*, 170, 795-806.

Sánchez-Gómez D., Zavala M.A. & Valladares F. (2008). Functional traits and plasticity linked to seedlings' performance under shade and drought in Mediterranean woody species. *Annals of Forest Science*, 65, 1.

Schiøtz M., Boesen M., Nabe-Nielsen J., Sørensen M. & Kollmann J. (2006). Regeneration in< i> Terminalia oblonga</i>(Combretaceae)—A common timber tree from a humid tropical forest (La Chonta, Bolivia). *Forest ecology and management*, 225, 306-312.

Schneider C.A., Rasband W.S. & Eliceiri K.W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671-675.

Searson M.J., Thomas D.S., Montagu K.D. & Conroy J.P. (2004). Wood density and anatomy of water-limited eucalypts. *Tree physiology*, 24, 1295-1302.

Sheffield J. & Wood E.F. (2007). Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Climate Dynamics*, 31, 79-105.

Sheffield J. & Wood E.F. (2008). Projected changes in drought occurrence under future global warming from multi-model, multi-scenario, IPCC AR4 simulations. *Climate Dynamics*, 31, 79-105.

Sims D. & Pearcy R. (1994). Scaling sun and shade photosynthetic acclimation of Alocasia macrorrhiza to whole-plant performance–I. Carbon balance and allocation at different daily photon flux densities. *Plant, Cell & Environment*, 17, 881-887.

Slot M. & Poorter L. (2007). Diversity of tropical tree seedling responses to drought. *Biotropica*, 39, 683-690.

Smith T. & Huston M. (1989) A theory of the spatial and temporal dynamics of plant communities. Plant Ecology 83, 49-69.

Sterck F. & Schieving F. (2011). Modelling functional trait acclimation for trees of different height in a forest light gradient: emergent patterns driven by carbon gain maximization. *Tree physiology*, 31, 1024-37.

Sterck F., Markesteijn L., Toledo M., Schieving F. & Poorter L. (2014) Sapling performance along resource gradients drives tree species distributions within and across tropical forests. *Ecology* in press.

Swaine M. (1996). Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology*, 84, 419-428.

Swaine M. & Whitmore T. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio*, 75, 81-86.

Swaine M.D., Agyeman V.K., Kyereh B., Orgle T.K., Thompson J. & Veenendaal E.M. (1997). *Ecology of forest trees in Ghana*. ODA, London. 76 pp.

Swaine M.D. & Becker P. (1999). Woody life-form composition and association on rainfall and soil fertility gradients in Ghana. *Plant ecology*, 145, 167-173.

Swets J.A. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240, 1285-1293.

ter Braak C.J. & Looman C.W. (1986). Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio*, 65, 3-11.

ter Steege H., Pitman N.C., Phillips O.L., Chave J., Sabatier D., Duque A., Molino J.F., Prevost M.F., Spichiger R., Castellanos H., von Hildebrand P. & Vasquez R. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*, 443, 444-7.

Thomas C. & Davis S. (1989). Recovery patterns of three chaparral shrub species after wildfire. *Oecologia*, 80, 309-320.

Timmermann A., Oberhuber J., Bacher A., Esch M., Latif M. & Roeckner E. (1999). Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, 398, 694-697.

Tobin M.F., Lopez O.R. & Kursar T.A. (1999). Responses of Tropical Understory Plants to a Severe Drought: Tolerance and Avoidance of Water Stress1. *Biotropica*, 31, 570-578.

Toledo M., Peña-Claros M., Bongers F., Alarcón A., Balcázar J., Chuviña J., Leaño C., Licona J.C. & Poorter L. (2012). Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology*, 100, 253-263.

Toledo M., Poorter L., Peña-Claros M., Alarcón A., Balcázar J., Chuviña J., Leaño C., Licona J.C., ter Steege H. & Bongers F. (2011). Patterns and determinants of floristic variation across lowland forests of Bolivia. *Biotropica*, 43, 405-413.

Tserenpurev B., Shinoda M. & Tsubo M. (2012). Effects of cloud, atmospheric water vapor, and dust on photosynthetically active radiation and total solar radiation in a Mongolian grassland. *Journal of Arid Land*, 4, 349-356.

Tyree M. & Hammel H. (1972). The measurement of the turgor pressure and the water relations of plants by the pressure-bomb technique. *Journal of Experimental Botany*, 23, 267-282.

Tyree M.T. (2003). Desiccation Tolerance of Five Tropical Seedlings in Panama. Relationship to a Field Assessment of Drought Performance. *Plant physiology*, 132, 1439-1447.

Tyree M.T., Engelbrecht B.M., Vargas G. & Kursar T.A. (2003). Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant physiology*, 132, 1439-1447.

Tyree M.T., Vargas G., Engelbrecht B.M. & Kursar T.A. (2002). Drought until death do us part: a case study of the desiccation-tolerance of a tropical moist forest seedling-tree, Licania platypus (Hemsl.) Fritsch. *Journal of Experimental Botany*, 53, 2239-2247.

Valladares F. (2003). Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. In: *Progress in Botany*. Springer, pp. 439-471.

Valladares F. (2004). Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. *Plant Biology,* 6, 254-268.

Valladares F., Arrieta S., Aranda I., Lorenzo D., Sánchez-Gómez D., Tena D., Suárez F. & Pardos J.A. (2005). Shade tolerance, photoinhibition sensitivity and phenotypic plasticity of Ilex aquifolium in continental Mediterranean sites. *Tree physiology,* 25, 1041-1052.

Valladares F., Gianoli E. & Gómez J.M. (2007). Ecological limits to plant phenotypic plasticity. *New Phytologist,* 176, 749-763.

Valladares F. & Pearcy R. (2002). Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. *Plant, Cell & Environment,* 25, 749-759.

Valladares F., SANCHEZ-GOMEZ D. & Zavala M.A. (2006). Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology,* 94, 1103-1116.

Valladares F., Wright S.J., Lasso E., Kitajima K. & Pearcy R.W. (2000). Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology,* 81, 1925-1936.

van der Waal C., de Kroon H., de Boer W.F., Heitkönig I.M.A., Skidmore A.K., de Knegt H.J., van Langevelde F., van Wieren S.E., Grant R.C., Page B.R., Slotow R., Kohi E.M., Mwakiwa E. & Prins H.H.T. (2009). Water and nutrients alter herbaceous competitive effects on tree seedlings in a semi-arid savanna. *Journal of Ecology,* 97, 430-439.

Van Gelder H.A., Poorter L. & Sterck F.J. (2006). Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist,* 171, 367-378.

Veenendaal EM., Swaine M.D., Agyeman V., Blay D., Abebrese I. & Mullins C. (1996a). Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology,* 84, 83-90.

Veenendaal E.M., Swaine M.D., Blay D., Yelifari N. & Mullins C. (1996b). Seasonal and long-term soil water regime in West African tropical forest. *Journal of Vegetation Science,* 7, 473-482.

Veenendaal E.M., Swaine M.D., Lecha R., Walsh M., Aberbrese I. & Owusu-Afriyie K. (1996c). Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology,* 10, 501-511.

Veenendaal E.M. & Swaine M. D. (1998). Limits to trees species distribution in lowland tropical rain forest. Pp. 163-191 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds.). *Dynamics of tropical communities*. The 37th Symposium of the British Ecological Society. Blackwell Science, Oxford.

Vesk P.A. (2013). How traits determine species responses to environmental gradients. *Journal of Vegetation Science*, 24, 977-978.

Vincens A., Schwartz D., Elenga H., Reynaud-Farrera I., Alexandre A., Bertaux J., Mariotti A., Martin L., Meunier J.D. & Nguetsop F. (1999). Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes. *Journal of Biogeography*, 26, 879-885.

Violle C., Navas M.-L., Vile D., Kazakou E., Fortunel C., Hummel I. & Garnier E. (2007). Let the concept of trait be functional! *Oikos*, 116, 882-892.

Vlam M., Baker P.J., Bunyavejchewin S. & Zuidema P.A. (2014). Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. *Oecologia*, 174, 1449-1461.

Walsh R. & Newbery D. (1999). The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 354, 1869-1883.

Walters M.B. & Reich P.B. (1999). Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytologist*, 143, 143-154.

Webb C.O. & Peart D.R. (2000). Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, 88, 464-478.

Westoby M. & Wright I.J. (2006). Land-plant ecology on the basis of functional traits. *Trends in ecology & evolution*, 21, 261-8.

Whitmore T. & Brown N.D. (1996). Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 351, 1195-1203.

Wieringa J., Poorter L., Bongers F., Kouamé F. & Hawthorne W. (2004). Biodiversity hotspots in West Africa; patterns and causes. *Biodiversity of West African forests: an ecological atlas of woody plant species*, 61-72.

Wilson P.J., Thompson K.E.N. & Hodgson J.G. (1999). Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, 143, 155-162.

Wood T.E., Detto M. & Silver W.L. (2013). Sensitivity of Soil Respiration to Variability in Soil Moisture and Temperature in a Humid Tropical Forest. *PloS one*, 8, e80965.

Wright I.J., Reich P. & Westoby M. (2001). Strategy shifts in leaf physiology, structure and nutrient content between species of high-and low-rainfall and high-and low-nutrient habitats. *Functional Ecology*, 15, 423-434.

Wright I.J., Reich P.B., Westoby M., Ackerly D.D., Baruch Z., Bongers F., Cavender-Bares J., Chapin T., Cornelissen J.H.C., Diemer M., Flexas J., Garnier E., Groom P.K., Gulias J., Hikosaka K., Lamont B.B., Lee T., Lee W., Lusk C., Midgley J.J., Navas M.-L., Niinemets U., Oleksyn J., Osada N., Poorter H., Poot P., Prior L., Pyankov V.I., Roumet C., Thomas S.C., Tjoelker M.G., Veneklaas E.J. & Villar R. (2004). The worldwide leaf economics spectrum. 428, 821-827.

Wright I.J. & Westoby M. (2002). Leaves at low versus high rainfall: coordination of structure, lifespan and physiology. *New Phytologist*, 155, 403-416.

Wright S.J. (1992). Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends in ecology & evolution*, 7, 260-263.

Wright S.J. (2010). The future of tropical forests. *Annals of the New York Academy of Sciences*, 1195, 1-27.

Wright S.J. & Cornejo F.H. (1990). Seasonal drought and leaf fall in a tropical forest. *Ecology*, 71, 1165-1175.

Wright S.J., Kitajima K., Kraft N.J., Reich P.B., Wright I.J., Bunker D.E., Condit R., Dalling J.W., Davies S.J., Díaz S., Bettina M. J. Engelbrecht , Kyle E. Harms , Stephen P. Hubbell, Christian O. Marks, Maria C. Ruiz-Jaen, Cristina M. Salvador & Zanne a.A.E. (2010b). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, 91, 3664-3674.

Wright S.J., Machado J.L., Mulkey S.S. & Smith A.P. (1992). Drought acclimation among tropical forest shrubs (Psychotria, Rubiaceae). *Oecologia*, 89, 457-463.

Wright S.J., Muller-Landau H.C., Condit R. & Hubbell S.P. (2003). Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology*, 84, 3174-3185.

Wright S.J. & Van Schaik C.P. (1994). Light and the phenology of tropical trees. *American Naturalist*, 192-199.

Zuur A.F., Ieno E.N. & Elphick C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1, 3-14.

Summary

Tropical forests occur along a rainfall gradient, and this variation in water availability is viewed as the main driver of the distribution, composition and diversity of tropical tree species. Other factors such as soil nutrients, understorey light, pest and pathogens vary along the rainfall gradient and may, in combination, shape species distribution and forest functioning. Climatic factors have been found to be stronger drivers of species distribution than edaphic and biological factors. More recently, species sensitivity to drought has been found to influence the distribution of species as well. Over the past four decades, the annual amount of rainfall has decreased by 4% per decade in West Africa, and this was the fastest rate of change recorded worldwide within this period. In addition, climate change scenarios models predict a further decrease in the annual rainfall amount and an increase in the length of the dry season for tropical forests. Such decreases in rainfall may affect species distribution and forest functioning, but the effects are largely unknown.

The responses of individual tree species to water availability have not often been quantified, and are poorly understood, especially for most West African tree species. The majority of tropical forest species regenerate in the forest understory. Consequently, the interaction effects of light availability (shade) and water availability may also influence recruitment patterns and the future structure of the forest canopy. However, there are conflicting views as to the role that light availability plays in the response of plants to drought. Understanding what climatic factors are critical for species distribution, individual species responses to low water availability (drought), low light, and the underlying mechanisms is imperative as it can help to predict the potential impact of global change on forest communities.

To determine species responses to drought, and the underlying mechanisms, I addressed four questions: (1) What is the relative importance of rainfall and temperature on tree species distribution? (2) How do species acclimatise to drought and shade in terms of their physiology, morphology, growth and survival? (3) What morphological and physiological traits determine species drought performance and distribution? (4) How do seedling survival, growth and physiology in the field vary between dry and wet forests and does drought tolerance and growth determine species distribution along the rainfall gradient?

In Chapter 2, I evaluated the relative importance of rainfall and temperature for the distribution of individual species. I used species presence/absence data from 2505 1-ha plots systematically distributed over Ghana's forests and related this to four climatic variables (annual rainfall, rainfall seasonality, isothermality and temperature seasonality) generated from the Worldclim database. The distribution of 95% of 20 species was significantly associated with annual rainfall, 60% with rainfall seasonality, 45% with isothermality and 40% with temperature seasonality. Isothermality is the mean diurnal temperature range relative to annual temperature range. Values less than 100 indicate a smaller level of diurnal temperature variability relative to the temperature variability in a year. Annual rainfall and rainfall seasonality explained on average 22% of the variation (range = 0.5%-52%) in species distribution, whereas temperature explained 5% (range = 0.4%-24%). These results suggest that predicted decreases in annual rainfall may cause a shift in the distribution of most species rather than the predicted increase in temperature.

I evaluated the effects of drought and shade on seedling survival and growth, and on the plasticity of 11 underlying traits related to biomass allocation, morphology and physiology, that are important for seedling performance (Chapter 3). Ten species were exposed to combinations of seasonal drought (continuous watering versus withholding water for nine weeks) and shade (5% and 20% of full sunlight) in a greenhouse experiment. Within species, shade facilitated the survival of drought-exposed seedlings, because shading ameliorates the microclimatic conditions. This contrasts with theories that postulate a trade-off between shade tolerance and drought tolerance. Plants grown in the shade allocated relatively more biomass to leaves to enhance light capture in a light-limited environment, but this came at the expense of allocation to roots. At first sight, this trade-off in biomass allocation suggests that shaded plants cannot survive drought because of a limited root system (*trade-off hypothesis*). However, shaded plants compensated for the lower allocation to roots by constructing thin roots with a high specific root length (root length per unit root mass), leading to a similar capacity for water uptake as high-light plants. Most of the traits studied (60% of 11 traits) responded independently to shade and drought (i.e., there was no interaction effect of light and water). This uncoupling of the effects of shade and drought may allow species to specialize independently for shade and drought, and hence, for niche differentiation and species coexistence under a range of water and light conditions. These results also suggest that many species growing in the understory of tropical forests may be able to survive under the predicted increased frequency of drought.

To understand the mechanisms underlying drought tolerance and hence species distribution along rainfall gradient, I determined functional traits that best predict species drought performance and distribution (Chapter 4). Additionally, in the same chapter, I identified the strategies that are used by plants to deal with drought. I studied 24 Ghanaian species with different distributions along the rainfall gradient in a greenhouse experiment where seedlings were exposed to two light treatments (5% and 20% of full sunlight) and two watering treatments (watered daily and water withheld for nine weeks). I measured 16 morphological and physiological traits, and seedling growth and survival, and related these to species position along the rainfall gradient, using the species response curves to annual rainfall as quantified in chapter 2. The study showed that plant species exhibit two main axes of strategy variation namely: (1) dense tissues and physiological drought tolerance versus drought avoidance and height expansion, and (2) resource acquisition versus resource conservation. Fast-growing species showed mostly a *drought avoidance* (deciduousness) strategy whereas, shade-tolerant species and non-pioneer light demanding species showed *drought tolerance* (dense stems and high leaf dry matter content). Across species, drought survival increased with biomass allocation traits that enhance water uptake (high plant biomass fraction in roots) and reduce water loss (low plant biomass fraction in leaves) and increased with the toughness of leaf- stem- and root tissues that enable physiological drought tolerance. Specific leaf area (leaf area per unit leaf mass, SLA) was the best predictor of the minimum rainfall at which species occurred, and lower SLA was associated with species that occur in wetter sites. A low SLA in wet forests is most likely not an adaptation to drought, but an adaptation to shade (as low SLA enhances leaf longevity and hence, leaf time carbon gain) and herbivores (as low SLA leaves are physically better defended and less palatable). The mechanisms underlying drought survival and species distribution might not be similar, as the trait that best predicted species position on the rainfall gradient was different from the trait that best predicted drought survival. Overall, the results suggest that species drought survival and position on the rainfall gradient can be predicted from morphological, biomass allocation and tissue density traits.

In Chapter 5, I carried out a two-year reciprocal transplanting experiment in gaps in dry and wet forests in Ghana, with seedlings of 23 tree species with contrasting rainfall distributions (dry, ubiquitous, and wet). I evaluated seasonal patterns in environmental conditions, tested whether species performance (survival and growth) and physiology differed between dry and wet forests and whether species showed a home advantage. In addition, I tested whether species' drought survival and growth performance were related to species' position on the rainfall gradient. Seasonal drought was higher in the dry forest than wet forest and led to a reduction in physiological plant activity, such as a lower leaf water potential and stomatal conductance. The reduction in physiological activity caused a reduction in carbon assimilation and hence lower growth. Consequently, growth was lower in the dry forest than the wet forest. Dry forest species showed a home-advantage, and realised higher survival and growth than wet forest species, not only in the dry forest but also in the wet forest. The ratio of species survival in the dry forest relative to the wet forest correlated negatively with species position on the rainfall gradient, and the same applied to growth rate. These results indicate that species that survive and grow relatively well under dry conditions occur in drier areas, and that drought performance plays an important role in species distribution. Hence, the predicted increase in frequency and intensity of drought due to climate change is likely to cause a shift in the distribution of species that occur at the wetter end of the rainfall gradient.

One central message that has emerged from this research is that water availbility in tropical forests plays a stronger role in shaping a species distribution than temperature, soil or pests. Trade-offs between drought avoidance, physiological drought tolerance, and drought intolerance strategies as identified in this study may act in combination with the spatial and temporal variation in water availability and disturbance regimes to shape species distribution and coexistence. Functional traits related to morphology, biomass allocation and tissue density are good and easy to measure proxies for determing a species drought tolerance and position on the rainfall gradient, when more complicated physiological measurements are difficult to make. Many of the species studied, showed a low to intermediate tolerance to drought. Consequently species tolerance to drought should be one of the criteria for selecting species for forest rehabilitation programmes. Finally, corridors should be established between fragmented forest sites to allow for potential shifts of species in response to the predicted increases in frequency and intensity of drought in the future.

Samenvatting

Tropische bossen komen voor langs gradiënten van regenval. Waterbeschikbaarheid is één van de belangrijkste factoren die de verspreiding en samenstelling van tropische boomsoorten- en daarmee de soortsdiversiteit van tropische bossen bepaalt. Andere variabelen zoals bodemnutriënten, licht, ziekten en plagen variëren ook langs deze regenvalgradiënt, en gezamenlijk bepalen zij de verspreiding van soorten en het functioneren van bossen. Recent onderzoek heeft laten zien dat de droogte aanpassingen van soorten ook van invloed is op hun verspreiding. In West Afrika is de afgelopen veertig jaar de jaarlijkse hoeveelheid regen met vier procent per tien jaar afgenomen; deze afname was de snelste verandering die was waargenomen in de tropen gedurende deze periode. Klimaatscenario's voorspellen bovendien dat de jaarlijkse regenval nog verder zal afnemen en dat de lengte van het droge seizoen in tropische bossen zal toenemen. Een dergelijke afname in regenval kan de verspreiding van soorten en het functioneren van bossen beïnvloeden, maar de precieze effecten zijn nog grotendeels onbekend.

De wijze waarop verschillende boomsoorten reageren op waterbeschikbaarheid is nog niet vaak gekwantificeerd, en er is weinig over bekend, vooral voor het merendeel van de West Afrikaanse boomsoorten. Doordat het grootste deel van tropische boomsoorten zich verjongt in de onderlaag van het bos, kan ook de wisselwerking tussen de beschikbaarheid van licht en water van invloed zijn op verjonging en de toekomstige samenstelling en structuur van het kronendak. Er zijn echter tegenstrijdige visies op de rol van licht in de reacties van planten op droogte. Om deze reden is het noodzakelijk om te begrijpen welke klimaatsfactoren bepalend zijn voor de verspreiding van soorten, hoe individuele soorten reageren op droogte en licht, en welke mechanismen hieraan ten grondslag liggen. Deze kennis kan een bijdrage leveren aan het voorspellen van de mogelijke impact van veranderingen in het klimaat op bossen.

Om te bepalen hoe boomsoorten reageren op droogte en de onderliggende mechanismen hiervan te begrijpen, heb ik in dit proefschrift vier vragen behandeld: 1) Hoe belangrijk zijn regenval en temperatuur voor de verspreiding van boomsoorten? 2) Hoe passen planten hun morfologie en fysiologie aan aan droogte en schaduw? 3) Welke morfologische en fysiologische kenmerken bepalen de overleving van soorten tijdens droogte en hoe bepalen deze kenmerken de geografische verspreiding van de soorten? 4) Hoe verschillen de overleving, groei en fysiologie van kiemplanten in nat en droog bos, en bepalen droogtetolerantie en groei de verspreiding van soorten langs de regenvalgradiënt?

In hoofdstuk 2 heb ik het belang van regenval en temperatuur voor de verspreiding van individuele soorten onderzocht. Soortsverspreiding is geanalyseerd in termen van aan- en afwezigheid van de 20 boomsoorten in 2505 proefperken van 1 hectare, die systematisch waren uitgelegd over de bossen van Ghana. Deze data heb ik gerelateerd aan vier klimaatsvariabelen die verkregen zijn uit de WorldClim database: jaarlijkse regenval, seizoensgebondenheid van regen, seizoensgebondenheid van temperatuur, en isothermaliteit (het gemiddelde bereik van de dagtemperatuur in verhouding tot het bereik van de jaarlijkse temperatuur).

De verspreiding van 95% van de bestudeerde 20 soorten was significant gerelateerd aan jaarlijkse regenval. Daarnaast was de verspreiding van 60% van deze soorten gerelateerd aan seizoensgebondenheid van regenval, 45% aan isothermaliteit, en 40% aan de seizoensgebondenheid van temperatuur. De jaarlijkse regenval en de seizoensgebondenheid van regenval verklaarden gemiddeld 22% van de variatie in de soortsverspreiding (bereik = 0.5% - 52%), terwijl temperatuur 5% (bereik = 0.4% – 24%) verklaarde. Deze resultaten suggereren dat vooral de voorspelde afname in jaarlijkse regenval, en niet zozeer de voorspelde temperatuurstijging, een verandering in de verspreiding van de meeste soorten kan veroorzaken.

In hoofdstuk 3 heb ik de effecten van droogte en schaduw op de overleving, groei, en 11 onderliggende plantkenmerken van kiemplanten bestudeerd. Deze kenmerken hebben betrekking op de allocatie (verdeling van biomassa binnen een plant), morfologie en fysiologie, die tezamen het succes van kiemplanten bepalen. Kiemplanten van tien boomsoorten werden gedurende negen weken opgegroeid in een kas experiment onder verschillende droogte niveaus (voortdurend bewateren versus onthouding van water) en schaduw niveaus (5% en 20% van volledig zonlicht).

Schaduw had een positief effect op de overleving van zaailingen die aan droogte werden blootgesteld, door de gunstige werking van schaduw op het microklimaat. Deze bevinding is tegenstrijdig aan theorieën die veronderstellen dat schaduw-en droogte-tolerantie negatief gecorreleerd zijn, en veelal niet samengaan. Planten die in de schaduw groeiden, investeerden relatief meer biomassa in hun bladeren om meer licht op te vangen, maar deze investering ging ten koste van de biomassa die werd geïnvesteerd in de wortels. Op het eerste gezicht lijkt deze *trade-off* in investering in bladeren versus wortels te suggereren dat planten in de schaduw niet bestand zijn tegen droogte omdat hun wortelsysteem beperkt is (de *trade-off* hypothese). De planten in de schaduw hadden hun lage wortelbiomassa echter gecompenseerd door dunne wortels met een hoge specifieke wortellengte (wortellengte per eenheid wortelmassa) te produceren. Hierdoor hadden zij een vergelijkbare wortellengte per eenheid plantbiomassa, en daarmee een vergelijkbare wateropnamecapaciteit als de planten die in het licht groeiden. Schaduw en droogte hadden op de meeste plantkenmerken (60% van de 11 geëvalueerde kenmerken) een onafhankelijk effect (d.w.z., er was geen interactie-effect van licht en water op deze kenmerken). Doordat de effecten van schaduw en droogte op de plantkenmerken niet aan elkaar gekoppeld zijn, lijken soorten zich onafhankelijk te kunnen specialiseren voor schaduwrijke en voor droge omstandigheden. Dit kan leiden tot niche differentiatie, en tot het samenleven van verschillende soorten onder uiteenlopende water- en lichtomstandigheden.

In hoofdstuk 4 heb ik de functionele plantkenmerken geïdentificeerd die droogtetolerantie en soortsverspreiding het beste kunnen voorspellen. Daarnaast heb ik gekeken welke strategieën soorten gebruiken om met droogte om te gaan. Hierdoor kunnen we beter begrijpen welke mechanismen de droogtetolerantie van soorten, en hun verspreiding langs de regenvalgradiënt bepalen. In een kas-experiment heb ik 24 Ghanese boomsoorten bestudeerd die een verschillende verspreiding hebben langs de regenvalgradiënt. Kiemplanten werden voor negen weken blootgesteld aan twee lichtniveaus (5% en 20% van volledig zonlicht) en twee bewateringsniveaus (voortdurende bewatering versus onthouding van water). Aan deze kiemplanten heb ik 16 morfologische en fysiologische kenmerken gemeten. Deze gegevens heb ik vervolgens gerelateerd aan de positie van iedere soort langs de regenvalgradiënt (aan de hand van de reacties van deze soorten op de jaarlijkse regenval uit hoofdstuk 2).

Deze analyse toonde aan dat de verschillende boomsoorten langs twee strategie assen gepositioneerd kunnen worden, namelijk (1) compact en taai plantenweefsel wat samengaat met fysiologische droogtetolerantie versus droogte-mijding en een snelle hoogtegroei, en (2) het opnemen van hulpbronnen versus het behouden van hulpbronnen. Snelgroeiende soorten pasten meestal een *droogte-mijdende* strategie toe (het verliezen van blad), terwijl schaduwtolerante soorten en lichtminnende soorten die halverwege de successie voorkomen ("lichtminnende niet-pioniersoorten") veelal *droogte-tolerantie* vertoonden (dicht houtweefsel en een hoog droge-stof gehalte in de bladeren). Soorten die de droogte relatief goed overleefden waren soorten die meer biomassa investeerden in het opnemen van water (relatief veel wortelbiomassa) en hun waterverlies beperkten (relatief weinig bladbiomassa). Bovendien konden soorten de droogte beter weerstaan naarmate zij compactere en taaiere blad-, stam- en wortelweefsels hadden, hetgeen hun fysiologische droogtetolerantie ten goede kwam. Het specifiek bladoppervlak (bladoppervlak per eenheid bladmassa, SLA) was de beste voorspeller van de minimale regenval waarbij een soort nog voorkwam. Tegen de verwachting in, was een lage SLA geassocieerd met de soorten die in een natte omgeving voorkomen. De lage SLA van deze soorten in natte bossen is waarschijnlijk geen aanpassing aan droogte, maar een aanpassing aan schaduw (aangezien een lage SLA de levensduur van het blad verhoogt en daardoor ook de hoeveelheid koolstof die een blad opneemt) en een aanpassing aan herbivoren (omdat bladeren met een lage SLA fysiek beter verdedigd zijn en minder eetbaar zijn voor insecten).

De mechanismen die droogte-overleving en soortsverspreiding bepalen zijn wellicht niet hetzelfde: het plantkenmerk dat de positie van een soort langs de regenvalgradiënt het best voorspelde was niet gelijk aan het kenmerk dat overleving bij droogte het best voorspelde. De resultaten suggereren dat, in het algemeen, plantkenmerken die gerelateerd zijn aan de morfologie, biomassa allocatie en compact en taai plantweefsel gebruikt kunnen worden als indicatoren voor de droogte tolerantie van soorten en hun verspreiding langs de regenvalgradiënt.

In hoofdstuk 5 beschrijf ik een tweejarig transplantatie-experiment uitgevoerd in open plekken in een droog bos en een nat bos in Ghana. Hiervoor gebruikte ik de kiemplanten van 23 boomsoorten die voorkomen op plaatsen die verschillen in regenval (droog, nat) en enkele soorten die overal aanwezig zijn). Ik heb onderzocht hoe de omgevingsfactoren fluctueerden per seizoen, en ik heb getest of de groei, overleving en fysiologie van de soorten verschilde tussen natte en droge bossen, en of soorten een voordeel hadden in hun eigen (natte of droge) milieu. Daarnaast heb ik onderzocht of het vermogen van soorten om onder droge omstandigheden te overleven en groeien was gerelateerd aan hun verspreiding langs de regenvalgradiënt.

De lengte van het droge seizoen was langer in het droge bos dan in het natte bos, en dit verlaagde de fysiologische activiteiten van de zaailingen, zoals weergegeven in de bladwaterpotentiaal en in de geleidbaarheid van de huidmondjes in het blad. Deze lage fysiologische activiteit beperkte de koolstofassimilatie en daardoor de groei in het droge bos, vergeleken met het natte bos. De soorten van het droge bos hadden een voordeel in hun eigen omgeving en groeiden sneller en overleefden beter dan de soorten uit het natte bos, zowel in het droge, als in het natte bos. De verhouding tussen het overleven van soorten in het droge bos ten opzichte van het natte bos was negatief gecorreleerd met de positie van deze soorten langs de regenvalgradiënt, en hetzelfde gold voor de groeisnelheid. Deze resultaten tonen aan dat soorten die betrekkelijk goed kunnen overleven en groeien onder droge omstandigheden voorkomen in droge gebieden en dat het functioneren onder droge omstandigheden in het algemeen een belangrijke rol speelt in de verspreiding van soorten. De voorspelde toename in zowel de frequentie als de intensiteit van droogte ten gevolge van klimaatsverandering zal waarschijnlijk leiden tot migratie van soorten die nu voorkomen in de nattere gebieden.

Een essentiële boodschap van dit onderzoek is dat de waterbeschikbaarheid in tropische bossen een grotere rol speelt in de verspreiding van soorten dan temperatuur, bodem of plagen. Ruimtelijke en temporele variatie in waterbeschikbaarheid en verstoringen, in combinatie met *trade-offs* tussen droogtestrategieën (droogtemijding, droogtetolerantie, en droogte–intolerantie) bepalen de verspreiding en het samenleven van boomsoorten. Fysiologische plantkenmerken zijn goede indicatoren van droogte tolerantie, maar relatief moeilijk te meten. Functionele plantkenmerken die betrekking hebben op de morfologie, de biomassa allocatie en de dichtheid van het plantweefsel zijn niet alleen goede maar ook makkelijk te meten indicatoren van de droogtetolerantie en positie van soorten langs de regenvalgradiënt. Veel van de soorten die hier bestudeerd zijn, zijn weinig tot gematigd droogte-tolerant. Daarom zou droogtetolerantie één van de selectiecriteria moeten zijn om soorten te selecteren voor bosherstelprogramma's. Tenslotte zouden er corridors moeten worden aangelegd tussen gefragmenteerde bosgebieden. Zulke corridors kunnen soorten in staat stellen te migreren naar betere plekken, als de frequentie en intensiteit van droogte in de toekomst zal toenemen.

Acknowledgements

I had always wanted to undertake a PhD study and anticipated it will be a challenging endeavor but somehow I had underestimated the cost of pursuing this study. I am happy this journey has come to a successful end. I thank the Netherlands Fellowship Programme (NUFFIC) and Wageningen University Sandwich Fellowship for the opportunity and support to carry out this study.

I would like to express my gratitude to the many people whose invaluable contributions have brought my PhD study to a successful end. The heartfelt thanks that I offer here is an inadequate measure of what their support has meant to me. Among the many people, my greatest gratitude is to my promoter Prof. Frits Mohren for accepting to support my PhD application when I first showed him the concept notes for the research and indicated my interest to be a PhD student at the Forest Ecology and Forest Management Chair Group (FEM). Thank you for the confidence you showed in me. I will never forget the first day I arrived in the Netherlands; you picked me up from the airport and made sure my first day at the University was as smooth as possible. Throughout my studies you supported any application I made to secure additional funds for the field work. I sincerely appreciate your guidance, encouragement, criticism and faith in me during my studies. At the last week to the submission of the thesis, you were on holidays but you still made time to read the full thesis and made your last comments. Thank you very much.

Prof. Lourens Poorter, in my candid opinion this PhD project would not have been accomplished at this time without your support. Your valuable contributions are reflected in the chapters of this thesis. Reflecting back, I have acquired a great deal of knowledge and skill under your supervision. I have kept the very first comments you made on my research proposal as a souvenir because of the depth of the comments you made. The comments greatly sharpened the focus of the research. I appreciate your patience and tolerance to my inadequacies and the relentless efforts you made to help me improve my skill in data analysis, interpretation and scientific writing. The countless times you passed by my office to check on the data and the analysis and 'baptised' them, the speed (at an average of 3 days) with which you gave me comments on the chapters of the thesis and the depth of discussion we had every Thursday of the week concerning the direction of the thesis was most inspiring. The week to submission was particularly busy for you yet you reviewed the chapters of the thesis for the last time. Thank you so much for the extra time you made in giving me comments despite your busy schedule. I must mention the many good memories I shared with you and your family. Uncharacteristic of me, I recall that at the height of the busy times, I had not planned any celebration for my birthday but you and your gracious wife invited me to your home for dinner and to my surprise you had baked a birthday cake and decorated it with candles. I thank you and your family for all the support.

Special thanks go to Prof. Frans Bongers for his continuous support throughout my study. I began the PhD application process with Prof. Mohren and you. Although you officially were no longer able to be my official supervisor due to other assignments, you continued to show interest in the project and its progress; you read and gave comments on almost all the empirical chapters of the thesis. Not only did I receive critical comments from you but you also gave them to me promptly despite your busy schedule. I really appreciate your steadfast efforts to the success of my PhD study.

I would like to thank my home supervisor Dr. Boateng Kyereh for the interest and continued guidance that helped in the successful completion of the thesis. Thank you very much for accepting to be my home supervisor upon reading the concept notes for this research. The comments you gave me tremendously helped in developing the concept notes. I also thank you for the constructive advice on the field work and comments on the empirical chapters of the thesis.
I greatly thank Dr. William D. Hawthorne for given me the permission to use the Ghana inventory data summarized by him and his constructive comments on the second chapter of this thesis.

The field work was extremely challenging, but I received the help of very dedicated people. I thank William Hagan Brown for assistance with the measurements in the field, and especially in the greenhouse experiments and data entry, and helping to take care of the experiments for most part of the PhD research. I thank Mr. Elvis Nkrumah and Nana Prempeh Bandoh for the many trips to Abofour and Benso/Bonsa for data collection; the number of times Elvis, you had to walk on all the plots to take the light measurements and Nana all the long drive and also staying in the sun outside the forest to take the light measurements. I greatly appreciate all your help. Certainly, I sometimes had to push you far beyond your limits when we were in the field but I am sure you're all happy this project has come to a successful end. I thank Mr. Peter Amoako for his support throughout the field work and especially at the early stages. We travelled together to a number of forest reserves looking for seeds of 23 tree species, which was an enormous task but we managed and got all the seedlings ready for the experiments. I did not complete the PhD study before you went on retirement but I'm sure you will be pleased that all the toil in the forest yielded good results. I thank Forestry Research Institute of Ghana's (FORIG) field staff at Abofour: Mr. Samuel Kyei, Kwaku Wiafe and at Benso/Bonsa; Mr. Mark Debrah, Mr. Francis Amo, Mr. Kwame Oduro and Rev T.T. Krah. The field work wouldn't have been successful without the help of all of you. I also thank all the national service personnel who worked with me and others who came in temporary to help with my field work; Emmanuel Agyare, Dorcas Gyimah Owusu, Eric Agyekum and Daniel Osei Owusu.

I thank my employer; Council for Scientific and Industrial Research (CSIR) for granting me the study leave to enable me undertake the PhD studies, CSIR-FORIG for institutional and logistical support and the director of FORIG, Dr. Victor Agyeman for his unwavering support throughout the study. I would also like to thank all FORIG staff, Dr. Adu-Bredu, Dr. Luke Anglaaere, Dr. Emmanuel Ebanyenle, Mr. Jonathan Dabo, Dr. Paul Bosu, Dr. Opuni-Frimpong, Dr. Owusu-Afriyie, Mr. Wilson Owusu, Akwasi Duah Gyamfi, Mrs. Theresa Peprah, Mrs. Bridgette Brentuo, Mrs. Gloria Djagbletey, Mrs. Sraku-Lartey, Mrs. Sarah Paintsil, Mrs. Britwum Acquah, Mrs. Elizabeth Obeng, Dr. Mrs. Mary Apetorgbor and Dr. Mrs. Darko Obiri for all the support and encouragement.

In the Netherlands, at Wageningen University I was very fortunate to have worked in a very wonderful research group (FEM). Everybody was willing to help. The staff of the FEM group made the students, especially the international students feel at home. They organized many extra curriculum activities to reduce a bit of the work pressure. This was very unique to the group and such outings were refreshing. I especially thank Mrs. Joke Jansen who had to organize our trips in and out of the Netherlands as well as other logistics. I thank all the staff, Dr. Danaë Rozendaal, Ms. Ellen Boerstra-Wilderink, Dr. Frank Sterck, Dr. Jan den Ouden, Mr. Leo Goudzwaard, Dr. Marielos Peña Claros, Prof. Pieter Zuidema, Dr. Ute Sass-Klaassen and Dr. Venceslas Goudiaby. I extend my gratitude to the other staff of Wageningen University; Patricia Meijer, Karin van der Goot, Marion Rodenburg, Dr. Claudius van de Vijver for all the administrative and academic and logistical support. And to the current PhD colleagues and those PhD students I met when I began my studies but who have now completed, I say thank you all for your friendship: Paul Copini, Helen Esser, Peter Groenendijk, Catarina Jakovac, Merel Jansen, Madelon Lohbeck, Huicui Lu, Estela Quintero Vallejo, Masha van der Sande, Marlene Soriano Candia, Lennart Suselbeek, Ha van Tiep, Monique Weemstra, Kwame Oduro, Canisius Mugunga, Dr. Lars Markesteijn, Dr. Meenaksi Kaul, Dr. Marisol Toledo, Dr. Coneille Ewango, Dr. Emiru Birhane Hizikias, Dr. Gabriel Muturi, Dr. Geovana Carreño-Rocabado, Dr. Jean Ndayambaje, Dr. Motuma Tolera Feyissa, Dr. Mart Vlam and Dr. Peter van der Sleen. I specially thank my Paranymhs Estela Quintero Vallejo and Caterina Jakovac for proof reading some of my chapters, Monique Weemstra for translating the summary of the thesis from English to Dutch and Dr. Joy Burrough-Boenisch for language advice.

In the Netherlands, I attended church at Amazing Grace Parish. I greatly thank the head pastor Pastor Dr. Farai Maphosa and his wife as well as the other leaders and members of the church for the good company that I enjoyed during my stay. I would like to thank the whole Ghanaian student community (Sikaman) at Wageningen University and my colleague female Ghanaian PhD students; Betty Adjei, Rose Omari, Joyce Halegoah, and Dr. Lilian Ayete-Nyampong for their friendship and support. I would also like to thank Ms. Monica Akanyinte and Steven Hoek for showing interest in my welfare. I am very grateful to Linda Grace Ennison, Mrs. Adwoa Waldburg, Mrs. Joana Beulah Echeruo, Mr. Ben Rockson, Dr. and Dr. Mrs. Nene Kodzi, Mr. and Mrs. Kwakye Donkor, Rev and Mrs. Wobir Nkrumah, Rev Kow Egyir, Mr. Kofi Atua Ntow, and Mr. Lawrence Akpalu for showing interest in my progress.

I greatly thank my parents for sending me to school to lay the foundation for this achievement and my sisters; Ewurama and Marian for showing interest in my work. Finally, I will like to thank my husband, Kodwo for your unconditional support and the sacrifice you had to make. On many occasions I was away in the field or in the Netherlands, and left you alone to take care of three young girls. You did all of these with dedication. I thank you for the peace of mind you gave me throughout the PhD studies so I could concentrate. And to my daughters:

Marilyn, Emmanuela and Michelle, words cannot express how grateful I am to you that you stayed good and managed my absence all these years. Emmanuela, the occasional text messages you sent to me were inspiring. I remember one of your text messages that so much encouraged me. In the message you wrote ‘Mummy I love you, may your dream come true’. The dream has indeed come true!

Short biography

Lucy Amissah was born on 21st of August 1969 in Elmina in the Central Region of Ghana. She attended St James Anglican Primary School and Dr. Baffour Middle School. For her secondary school education, she attended Ghana National College for her Ordinary level certificate (from 1985-1989) and attended Wesley Girls High School Cape Coast where she obtained her Advance level certificate in Physics, Chemistry and Biology in 1991. In 1993, she joined the Institute of Renewable Natural Resources at the Kwame Nkrumah University of Science and Technology and graduated in 1997 with a Bachelor of Science honors degree in Natural Resources Management with a major in Forestry. In 1999 she enrolled at the same University for her master's degree and completed in 2003 with an MPhil degree in Silviculture and Forest Management. For her MPhil research she worked on the topic 'effects of wildfire on farming system dynamics in the forest transition zone of Ghana'. The results of the research were published in Ghana Journal of Forestry. Whilst working on her MPhil degree she worked as a project assistant and coordinated a three-year International Tropical Timber Organization funded forest fire management in Ghana project (ITTO PD. 32/98 Rev. 1F) that was implemented by CSIR-FORIG. Her job entailed, writing of project progress and technical reports and project correspondence. Additionally, she led the research on the aspect of the project that focused on farming systems impact on forest fire occurrence. From 2000-2004, she attended courses on biodiversity assessment and monitoring, environmental leadership at Monitoring and Assessment of Biodiversity Program of the Smithsonian Institution, Virginia and prescribed burning training at the Prescribe Burning Training Academy, Tallahassee, Florida in the United States of America. She also attended Tropical Biology Association field courses (1998) in Uganda and Earth watch vegetation survey course (1999) in Zambia. Through these courses she developed a strong interest in forest ecology.

In February 2004, she was employed by the Council for Scientific and Industrial Research -Forestry Research Institute of Ghana (CSIR-FORIG) as a Research

Scientist, a position she has held to date. She conducts her research within the Biodiversity and Land Use Division of CSIR-FORIG. Past projects carried out by her include assessment of plant diversity and regeneration in tree plantation, role of fire in farming systems in forest transition zone and development of improve systems of farming and effects of drought on survival and growth of agricultural tree crops in Ghana.

In 2009, She Started a Sandwich PhD studies at Wageningen University in the Forest Ecology and Forest Management Group and studied functional traits influence on drought survival and tree species distribution in Ghana. She got married to John Kodwo Amissah in 1998 and has three daughters; Marilyn, Emmanuela and Michelle.

List of publications

Amissah, L., Mohren, G. M. J., Bongers, F., Hawthorne, W. D., Poorter, L. 2014. Rainfall and temperature affect tree species distribution in Ghana. *Journal of Tropical Ecology* 30, 435-446.

Amissah, L., Kyereh, B., Agyeman, V. K. 2011. Wildfire as dominant force driving farming systems in the forest transition zone of Ghana. *Ghana Journal of Forestry* Volume 27, 52-65.

Amissah, L., Kyereh, B., Agyeman, V. K. 2010. Wildfire incidence and management in the forest transition zone of Ghana: Farmers' perspectives. *Ghana Journal of Forestry* Volume 26, 61-73.

Amissah, L. 2009. Indigenous fire management practices in Ghana. In: Parrotta, J. A, Oteng-Yeboah, A., Cobbinah, J. (eds). Traditional Forest-Related Knowledge and Sustainable Forest Management in Africa. *IUFRO World Series*, Volume 23, 131-135.

Affiliations of Co-authors

Godefridus M. J. Mohren
Forest Ecology and Forest Management Group,
Wageningen University
Wageningen, the Netherlands

Lourens Poorter
Forest Ecology and Forest Management Group,
Wageningen University
Wageningen, the Netherlands

Boateng Kyereh
College of Agriculture and Natural Resources,
Kwame Nkrumah University of Science and Technology
Kumasi, Ghana.

Frans Bongers
Forest Ecology and Forest Management Group,
Wageningen University
Wageningen, the Netherlands

William D. Hawthorne
Department of Plant Sciences,
University of Oxford, South Parks Road,
Oxford, OX1 3RB, UK.

Victor K. Agyeman
CSIR-Forestry Research Institute of Ghana,
P.O Box UP63, KNUST, Kumasi,
Ghana

PhD Education Certificate

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Effects of environmental factors on tree regeneration in tropical forests (2010)

Writing of project proposal (4.5 ECTS)

- Effects of climate change on regeneration of tree species in tropical forest of Ghana (2009)

Post-graduate courses (4.7 ECTS)

- Understanding global environmental change: processes, compartments and interactions; SENSE (2009)
- Multivariate analysis; WGS (2012)
- Generalized linear models; WGS (2013)
- Mixed linear models; WGS (2013)

Deficiency, refresh, brush-up courses (3 ECTS)

- Ecological methods 1 (2011)

Competence strengthening / skills courses (3.9 ECTS)

- PhD \Competence assessment; WGS (2009)
- Information literacy, including introduction to EndNote; WGS (2009)
- Techniques for writing and presenting a scientific paper; WGS (2011)
- Scientific writing; WGS (2012)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.7 ECTS)

- PE&RC Weekend; first year's edition (2009)
- PE&RC Day (2009, 2011-2013)
- PE&RC Weekend; last year's edition (2014)

Discussion groups / local seminars / other scientific meetings (7.5 ECTS)

- Ecological theory and application (2009, 2011-2013)
- Forestry Research Institute of Ghana; weekly seminars (2010-2012)
- Tropical Ecology in the Netherlands; University of Amsterdam (2013)

International symposia, workshops and conferences (5.6 ECTS)

- XXIII International Union of Forest Research Organizations (IUFRO) World Congress; oral presentation; Seoul, South Korea (2010)
- ATBC Annual meeting; oral presentation; San José, Costa Rica (2013)

Supervision of MSc student (3 ECTS)

- Is herbivory associated with distribution of tropical trees along a rainfall gradient in Ghana?

The research contained in this thesis was financially supported by the Netherlands Fellowship Programme (NUFFIC); grant number CF7428/2011, Wageningen University Sandwich Fellowship and the Council for Scientific and Industrial Research-Forestry Research Institute of Ghana.

Cover: Photography by Lucy Amissah
Cover design: Arthur van Aken, Leeuwenkracht - Vormgeving en DTP, Zeist, The Netherlands

Layout: Ferdinand van Nispen, Citroenvlinder-DTP.nl, Bilthoven, The Netherlands
Printed by: GVO drukkers & vormgevers B.V. | Ponsen & Looijen, Ede, The Netherlands