Two decades of change in Ghanaian forests

Sophie Fauset

Submitted in accordance with the requirements for the
degree of
Doctor of Philosophy

The University of Leeds
School of Geography

May 2012

The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2:

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, 1120-1129.

SF, TRB, SLL, MDS, TRF and KCH designed the study; SF, TRF and EGF collected data; KA-B, SLL and MDS provided data; SF analysed data and wrote the paper.

Chapter 3:

In preparation. SF, TRB, SLL and TRF designed the study; SF and EGF collected data; KA-B, TRF and TROBIT consortium provided data; SF analysed data and wrote the paper.

Chapter 4:

In preparation. SF, TRB, SLL, TRF and KCH designed the study; SF, TRB and EGF collected data; KA-B, SLL and MDS provided data; SF analysed data and wrote the paper.

Assertion of moral rights:

The right of Sophie Fauset to be identified as Author of this work has been asserted by her in accordance with the Copyright, Designs and Patents Act 1988.

Acknowledgements

First, many thanks to my principal supervisor, Tim Baker, for the considerable support, guidance, ideas and time given to me over the course of this project. I also thank my supervisors Simon Lewis, Ted Feldpausch, Keith Hamer and Michael Krom for all their contributions.

This work could not have been carried out without the Forestry Commission of Ghana and the work put into the forest inventory network over the past decades from multiple field staff. Thank you to Kofi Affum-Baffoe for providing access to these resources, and the many forest guards, forest managers and local people for helping to locate the plots. Data from inventory plots were provided by the AFRITRON and TROBIT projects. Ernest Foli and the Forestry Research Institute of Ghana provided logistical support and guidance. I thank Jonathan Dabo for botanical assistance. Previous work on the ecology of Ghanaian tree species was essential to this thesis and I thank Michael Swaine and William Hawthorne for making this data available. Datasets on fire occurrence were provided by Rosa Maria Román Cuesta and France Gerard. Gabriela López-González provided assistance with the ForestPlots.net database, and Gloria Djabletey helped with exporting soil.

I am very grateful for all the funding received: the Earth and Biosphere Institute provided my studentship, and the Royal Society, Sebright's Educational Foundation and the Gilchrist Educational Trust funded the fieldwork.

I thank the laboratory staff, Rachel Gasior, Martin Gilpin, David Ashley, John Corr and Miles Ratcliffe, for patient training in soil preparation and analytical methods, as well as caring out some of the soil analyses.

I thank Oliver French for keeping me going. My family have always provided encouragement to me and even measured a few trees too! Thanks to the many

colleagues who have become friends and provided both fun and help along the way, in particular, the support, singing and general mischief in the basement provided by Katie Aspray and Michelle Johnson. The following people also deserve a special mention: Lindsay Banin, Tim Jones, Ed Turner, Katherine Dunlavy, Keith Bloomfield, Nikée Groot, Rosie Goodman, Kate Staines, Yanan Jiang and Simon Willcock.

The biggest thanks I have are for my amazing field team in Ghana. Kwaku Duah, Yaw Nkrumah and Justice Afedo Godwin were far more than I could have hoped for; hard working, supportive, loyal and kind. I have you to thank for the amazing experiences I have had and the work that was done, I think we made a great team.

Finally, I wish to dedicate this thesis to Kwaku, a fantastic friend, logistics manager, tree measurer, football fan, dancer, plot finder, rat catcher, spar player, joker and forester. You are deeply missed.

Kwaku Paul Duah

Abstract

Understanding the impacts and synergies of the many threats facing tropical forests is a key research challenge. Here, three potential threats are addressed: drought, fire and lianas. Using a network of 31 plots, changes attributed to these threats are addressed over two decades in Ghanaian forests.

Ghana experienced a multi-decade drought beginning in the early 1970s. The impact of this drought on functional composition and forest structure was tested. The results show clear shifts in functional composition. Despite this, biomass increased during the study period. This suggests that shifting species composition in favour of drought-tolerant species increases the resilience of tropical forests to long-term drought.

A strong El Niño event in 1983 led to widespread wildfires in the Ghanaian forest zone. To test the long-term impacts of these fires the structure and composition of seven burnt plots and three control plots were compared. 27 years after initial fires, stem density and biomass were reduced in burnt plots, and composition was characteristic of disturbed forest. Over the twenty year study period, forest structure showed evidence of regeneration, but no recovery of floristic composition was observed.

In contrast to the large increase in lianas observed in the Neotropics, there was only a very slight increase in the percentage of infested trees over the study period. Forest structure was found to be the main driver of liana spatial distribution. Importantly, large lianas showed different spatial patterns, as forest turnover was the strongest predictor of large liana distribution.

Overall, fire was found to be the strongest threat, having a large and long-term impact on forest structure and composition. The results highlight that the prevention of fire occurrence should be a priority in tropical forest regions, as should the maintenance of biodiversity to maximise the resilience of forest to external changes.

Table of Contents

List of Tables

List of Figures

1. Introduction

1.1 Threats to tropical forests

Tropical forests cover just 10 % of the Earth's surface but contain over 50 % of plant species (Mayaux *et al.* 2005). They are an important component of global biogeochemical cycles, and provide a myriad of ecosystem services (Constanza *et al.* 1997; Nasi *et al.* 2002). They also directly provide resources for many millions of people. In the current age of unprecedented influence on the planet by one species, potentially leading to the definition of a new geological epoch (Crutzen 2002), tropical forests face serious threats. However, the tropical forest biome has persisted for approximately 120 Myr (Davis *et al.* 2005). For their continued persistence through future changes, understanding of the impacts of the threats posed and appropriate management will be required.

Human activities influence tropical forests directly in many ways. The clearest of these is deforestation, the removal of forest vegetation to make way for other land uses such as agriculture or urbanisation. Globally, the footprint of deforestation is large; in 2005 remaining forest cover (> 50 % tree cover) in Africa and South America was estimated at 62.8 % and 63.8 % respectively and was considerably lower in Asia/Oceania (27.2 %) and Central America (26.9 %) (Asner *et al.* 2009). The global rate of forest clearance between 2000 and 2005 has been estimated at 1.4 % yr^{-1} (Asner *et al.* 2009). Deforestation has deeper impacts than simply removing forest area as it also affects regional hydrology and precipitation (Avissar *et al.* 2006). Global precipitation may also be affected; the majority of climate simulation experiments using global climate models (GCMs) with and without complete Amazon deforestation predict decreased precipitation with deforestation (Marengo 2007). Deforestation also leads to increased fragmentation of remaining forest, which elevates tree mortality and alters floristic composition within 100 m of forest boundaries (Laurance *et al.* 1997; 1998; 2006). Fragmentation is also increased by road building, which is of particular significance in locations with large remaining forest areas such as the Amazon and Central Africa. Road building improves access to forest resources and can lead to increases in deforestation, logging and hunting (Laurance *et al.* 2009). Hunting, which is particularly pervasive in the African tropics, has obvious impacts on forest fauna. Changes in faunal populations have subsequent impacts on forest flora due to the removal of large seed predators and seed dispersers (Wright *et al.* 2007; Terborgh *et al.* 2008). Selective logging of remaining forest, both legally and illegally harvested, causes degradation of the forest ecosystem. This is particularly true for intensive mechanised logging operations that involve the introduction of logging roads within forests. Collateral damage to other trees in addition to the tree being harvested is high (Johns 1988) and the damage caused by selective logging can leave forests exposed to further disturbances.

Physical disturbances to forests such selective as logging and fragmentation affect not only forest structure and composition but can also catalyse other disturbances. For example, fragment edges with large perimeters and more open and fuel-laden structures are at greater risk of fires during dry years (Laurance 2006). These fires can have severe impacts on forest structure and composition (Barlow & Peres 2006). Structurally damaged forests are also thought to be of higher risk of plant diseases (Benítez-Malvido & Lemus-Albor 2006) and invasion by exotic plant species (Fine 2002; Denslow & DeWalt 2008).

Human activities also impact tropical forests indirectly by, for example, climate change and increased concentrations of atmospheric CO_2. Rising temperatures are likely to have consequences for tropical trees as the rates of many physiological processes (e.g. respiration, photosynthesis) change with temperature. Climate change is also likely to alter precipitation patterns which in turn will also affect forest growth and mortality. Although there is variation in predictions of different regions, and future trends in some areas are not well understood at present, increased drought frequency, longevity and intensity are predicted by some GCMs (Christensen *et al.*, 2007). When linked to dynamic global vegetation models (DGVMs), some alarming results have been found, such as predicted dieback of the Amazon forest during the 21st century (Cox *et al.* 2004), particularly in the eastern portion of the basin (Malhi *et al.* 2009; Zelazowski *et al.* 2011). Strong drought events in recent decades have resulted in biomass loss in Amazonia (Phillips *et al.* 2009a; 2010; Lewis *et al.* 2011) and Asia (Slik 2004; van Nieuwstadt & Sheil 2005). Increases in atmospheric CO_2, however, may have a positive impact on tropical forest biomass stores. When including increased CO_2 in GCM-DGVM model runs, biomass losses due to future climate change are much reduced compared to runs without a CO_2 fertilisation effect (Lapola *et al.* 2009; Galbraith *et al.* 2010). Changes to forest structure tentatively linked to rising atmospheric CO_2 or increases in availability of other resources have been observed across extensive networks of monitoring plots in South America and Africa (Phillips *et al.* 1998; Baker *et al.* 2004a; Phillips *et al.* 2004; Lewis *et al.* 2004; Lewis *et al.* 2009a; Phillips *et al.* 2009a). These studies have shown increased biomass, basal area and tree turnover across the tropics, suggesting that forests are already responding to global environmental change. The abundance of lianas also increased in the Neotropics in recent decades (Phillips *et al.* 2002; Ingwell *et al.* 2010), hypothesised to be linked to global environmental change (Schnitzer & Bongers 2011).

The impacts of many of the threats and changes to tropical forests presented above are very uncertain. Prediction of the likely future trajectories of tropical forests requires a thorough understanding of all potential threats and synergies between them, and is necessary to guide policy makers on the best course of action for conservation. The synergies between threats to tropical forests, their likely impacts on forests and feedbacks between threats and impacts are shown diagrammatically in Fig. 1.1. This thesis uses long-term forest inventory datasets from Ghanaian tropical forests to address a number of the processes detailed in Fig. 1.1. In particular this thesis will assess the resilience of forests drought and fires, and changes in liana abundance (which could lead to increased tree mortality and changes to forest composition, see Section 1.4.2). These processes are associated with considerable uncertainty and the nature of the dataset and circumstances surrounding it allow in depth research. Specifically, I will test responses of forest composition and structure to a long-term drought (Chapter 2), the impact and recovery of forest structure and composition to wildfires (Chapter 3), and the recent temporal patterns of liana abundance and the drivers of liana spatial distribution (Chapter 4).

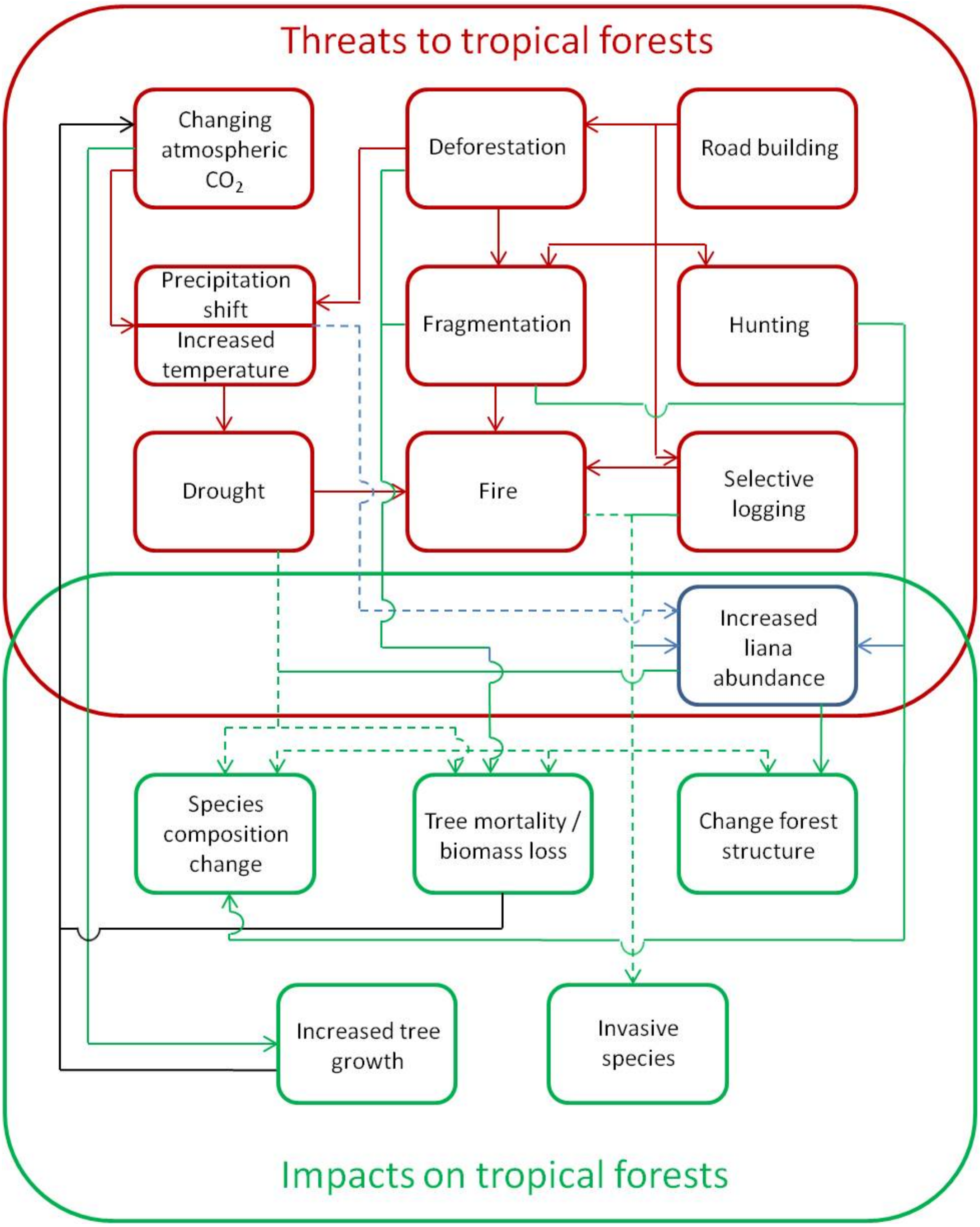

Figure 1.1. Conceptual model of the threats to tropical forests and their impacts. Threats are shown in red, with red arrows representing interactions between threats, impacts of threats are shown in green, increased liana abundance which could be considered both a threat and an impact is shown in blue and the feedback of tree mortality on increased atmospheric CO_2 concetration is shown in black. Dashed lines show the processes assessed in this thesis.

1.2 Droughts

1.2.1 Precipitation and water stress in tropical forest regions

The tropics receive two thirds of global annual rainfall (McGregor & Nieuwolt 1998) and precipitation in tropical moist forest areas ranges from 1200 - 10000 mm yr^{-1} (Hijmans *et al.* 2005). The dominant factor leading to high rainfall is the presence and length of stay of the intertropical convergence zone (ITCZ), whilst topography and cyclones are also important (McGregor & Nieuwolt 1998). South America and Asia have wetter climates than Africa (Hijmans *et al.* 2005). Seasonality also varies between tropical forest regions with areas of higher rainfall typically being less seasonal. Seasonality is lowest near the equator where the ITCZ provides a relatively constant influence (McGregor & Nieuwolt 1998). The movement of the ITCZ results in seasonality patterns, such as the typical bimodal rainfall pattern in much of Africa due to the passing over of the ITCZ twice a year, that vary in different locations (McGregor & Nieuwolt 1998).

Tropical precipitation also shows high inter-annual variability (Salinger 2005). This is often linked to El Niño Southern Oscillation (ENSO), with low rainfall in El Niño years (ENSO events). ENSO is a tied ocean-atmosphere process in which changes in Pacific sea surface temperatures alter atmospheric pressure and hence impact the climate system (McGregor & Nieuwolt 1998). The correlation between ENSO events and rainfall is particularly strong in South America and Asia and is weaker in Africa (Malhi & Wright 2004). Temperature increases in El Niño years in all tropical forest locations (Malhi & Wright 2004). ENSO is a complex process which can show nonlinear and extreme responses to small changes in controlling variables and therefore is difficult to accurately capture in climate models (Malhi & Wright 2004).

Droughts can be defined as below normal precipitation for periods that can last from months (e.g. ENSO related droughts) to years or even decades (Dai 2011). In terms of vegetation water stress, soil moisture deficit incorporating soil water holding capacity, evapotranspiration and precipitation has more impact than changes to precipitation *per se*. Soil water holding capacity is strongly determined by soil texture. For example, soils with high sand content will have large pore spaces between soil particles and water will drain easily through these pores; therefore less water will be retained in sandy soils compared with clay soils with smaller pore spaces (Shaw 1994). Spatial variation in soil properties can therefore result in variations in plant water stress even under the same precipitation regime. Evapotranspiration, the movement of water from soil to the atmosphere through plant stomata (Hendriks 2010), increases with temperature and therefore changes in temperature influence water stress. Water that is lost from soil through evapotranspiration or runoff can be recharged by precipitation. To account for these processes that influence plant water stress in tropical forests, the term maximum cumulative water deficit (MCWD) has been developed (Aragao *et al.* 2007). MCWD is a measure of drought severity representing the maximum amount of cumulative soil water deficit over the course of a year, based on the assumption that each month 100 mm of water is lost through evapotranspiration from tropical forest canopies (Shuttleworth 1989). MCWD varies spatially, reflecting differences in precipitation regimes and, in particular, differences in seasonal water stress. As described above, variation in seasonality between different regions occurs due to their position in relation to the ITCZ. This variation in water stress leads to the occurrence of different vegetation types with different species compositions, for example Malhi *et al.* (2009) show that in Amazonia forest vegetation occurs where MCWD is greater than -300 mm and annual precipitation is greater than 1500 mm yr^{-1}, whereas below these limits savanna occurs. The species occurring in different biomes are adapted to their local climatic conditions with varying seasonal drought strengths, and within the tropical forest biome species composition is known to vary over climatic gradients (Bongers *et al.* 1999; Engelbrecht *et al.* 2007). The species that occur in locations which typically experience seasonal water stress are able to cope with such conditions (see Section 1.2.2), and as such deviations from the typical precipitation regime of a region are more important than seasonal variations in the context of drought impacts on tropical forests.

Over the past 50 years temperatures have increased globally (Dai 2011), with a mean increase in tropical forest regions of 0.26°C decade^{-1} from 1976 to 1998 (Malhi & Wright 2004). Rainfall has declined in some areas over these timescales, particularly in Africa

(Malhi & Wright 2004; Dai 2011). Estimates of the Palmer Drought Severity Index for the period 1900 - 2008 shows long-term drying over Africa, East Asia and northern Amazonia (Dai 2011). Until the 1980s precipitation was found to be the dominant driver of drying trends, whereas after the early 1980s surface warming and solar radiation also became important (Dai 2011). Some forests may have experienced water stress in the last century, either directly due to reductions in precipitation or due to other changes. Future projections of the global climate show a high likelihood of increased temperatures over the next 50 - 100 years. Using eight IPCC AR4 models, Sheffield & Wood (2008) show global decreases in soil moisture by the end of the 21st century with a doubling of short (4 - 6 months) droughts, and a tripling of droughts lasting 12 months or more. Short droughts in particular may affect tropical forest regions, with tropical Africa and South America particularly at risk. Amazon specific analyses using more extensive ensembles of 19 - 24 models highlight the risk for Eastern Amazonia (Malhi *et al.* 2009) and Southern Amazonia (Cook *et al.* 2012). Given these predictions, it is important to understand the impacts of drought on tropical forests.

1.2.2. Impacts of droughts on tropical forests

Tropical forests are considered to be resilient to seasonal water stress that occurs as part of the typical precipitation regime (Davidson *et al.* 2012). For example, deep rooting systems reaching more than 8 m below the soil surface allow trees to maintain evapotranspiration and photosynthesis during seasonally dry periods (Nepstad *et al.* 1994). Further, such roots have been shown to redistribute deep water resources to shallower soils during the night to provide water to shallow roots during the day (Caldwell *et al.* 1998; Oliviera *et al.* 2005). Leaf phenology is also an important component of adaptations to seasonal water stress. The majority of leaf fall in seasonal tropical forests occurs during the dry season which may avoid the risk of experiencing dangerous levels of water stress at the end of the dry season when cumulative water deficits are highest (Wright & Cornejo 1990). Leaf physiology may also play a part in plant adaptations to seasonal water stress. Trees that retain their leaves during seasonal droughts have been found to show isohydric behaviour (Fisher *et al.* 2006), closing stomata to maintain leaf water potentials above a critical threshold (Field & Holbrook 1989). The adaptations mentioned here allow tropical trees to survive during seasonal water stress. The responses of forests to anomalous drought events, outside of the typical seasonal variation experienced by any site, is the focus of this section of the thesis. Due to the variation in background precipitation regimes, an anomalous drought may be very different in terms of precipitation reduction in different areas.

The initial impacts of drought on tree mortality have been assessed in a number of studies, particularly focussed on strong ENSO droughts such as those that occurred in 1982/83 and 1997/98. For example, Woods (1989) found 12 - 28 % of trees in logged forests in Borneo died due to the 1982/83 ENSO drought and mortality was consistent between size classes (Woods 1989). Leighton & Wirawan (1986) also report increased mortality due to drought in Borneo with 14 - 24 % of trees dying. The 1982/83 ENSO event also affected Barro Colorado Island, Panama, but not as strongly as in the Bornean forests studied by Woods (1989) and Leighton & Warawan (1986). Condit *et al.* (1995) assessed tree mortality rates over the drought period 1982 - 1985 and post-drought period 1985 - 1990. During the drought an additional 2 % of stems ≥ 10 cm diameter died compared with post-drought. Canopy species were particularly affected.

The impacts of the 1997/98 ENSO event was well studied in Borneo where rainfall was severely reduced with several months receiving < 100 mm rainfall in an area that is typically everwet (Potts 2003, van Nieuwstadt & Sheil 2005). Nakagawa *et al.* (2000) found tree mortality rates increased from 0.89 % yr^{-1} pre-drought (1993 - 1997) to 6.37 % yr^{-1} during the drought. Similarly, basal area mortality rose from 0.33 % yr^{-1} pre-drought to 5.28 % during the drought. Additionally, pre-drought mortality was biased towards small trees, whereas drought mortality affected trees of all size classes (Nakagawa *et al.* 2000). Potts (2003) show similar results; tree mortality was three times higher during drought than pre-drought (1993 - 1997). Results from Slik (2004) show greater mortality; after the 1997/98 drought 15.4 % of stems were dead compared to 4.2 % during a four year post-drought period. Mortality was higher in disturbed forest; forests logged 24 years previously had drought-induced mortality of 19.6 %, and forests logged 14 years previously were even more severely affected with 25.7 % mortality. The discrepancy between forests of different disturbance histories was attributed to high mortality of pioneer trees of the *Macaranga* genus. Mortality was higher for trees growing areas of lower soil moisture, and for trees > 20 cm diameter compared with trees 10 - 20 cm diameter. Similarly high mortality (11 - 19 %) was reported by van Nieuwstadt & Sheil (2005), increasing further to 22 - 26 % cumulatively two years after drought. Larger trees were again found to suffer greater mortality. Furthermore, mortality varied between different species and species with lower wood density displayed greater mortality (van Nieuwstadt & Sheil 2005). In addition to increased mortality, studies have shown growth rates of surviving trees to be reduced during the drought period (Nakagawa *et al.* 2000; Newbery *et al.* 2011), but may then increase post-drought (Newbery *et al.* 2011). Impacts of the 1997/98 ENSO event in other regions were less severe. Despite a reduction in dry season rainfall in the central Amazon from the long-term average of 732 mm to 230 mm in 1997, mortality only increased to 1.94 % yr^{-1} from a background rate of 1.12 % yr^{-1} (Williamson *et al.* 2000). Similarly, at three sites in Panama mortality was only weakly enhanced during the 1997/98 ENSO event, and only significantly so at one site (mortality 1.23 % yr-1 1994 - 1997 vs. 1.70 % yr^{-1} 1997 - 1998, Condit *et al.* 2004).

More recently, widespread droughts have occurred in the Amazon during 2005 and 2010 (Marengo *et al.* 2008; Phillips *et al.* 2009a; Lewis *et al.* 2011). Phillips *et al.* (2009a) show large biomass losses compared to earlier multi-decadal biomass increases, based on a widespread network of monitoring plots. This result is mostly due to increased tree mortality, and marginally also to decreased tree growth (Phillips *et al.* 2009a). Furthermore, using data from the network of plots in combination with other datasets (many of which are cited above), Phillips *et al.* (2010) found large trees and those with low wood density are more susceptible to drought. At lower drought intensities mortality related linearly to intensity, whereas at higher intensities mortality increased disproportionately. Post-drought period mortality was lower than during the drought period, but not as low as pre-drought.

Drought experiments also provide insight into the impacts of reduced rainfall on tropical forests. However, at present only 2 ha of tropical forest have been experimentally droughted in two experiments. Throughfall exclusion (TFE) experiments involve the placement of plastic panels above the forest floor angled to transfer rainfall into channels to remove it from the plot (Nepstad *et al.* 2002; Fisher *et al.* 2007). Both experiments are located in eastern Amazonia, in Tapajos National Forest where throughfall exclusion panels were in place only during the wet season (Nepstad *et al.* 2002), while in Caxiuanã where panels were used throughout the year (Fisher *et al.* 2007). Results from the two experiments show a high level of consistency. In both cases tree mortality between TFE and nearby control plots did not greatly differ until three to four years after commencement of the experiment (Nepstad *et al.* 2007; Brando *et al.* 2008; da Costa *et al.* 2010) when soil water is substantially reduced. Over the whole study periods (5 years in Tapajos, 7 years in Caxiuanã) annual mortality rates of TFE plots were 5.7 % yr^{-1} and 2.5 % yr^{-1} in Tapajos and Caxiuanã respectively, compared to control plot mortality rates of 2.4 % yr^{-1} and 1.25 % yr^{-1}; in both experiments stem mortality under TFE were twice the rates in control plots (Brando *et al.* 2008; da Costa *et al.* 2010). Clear size-dependent mortality was also consistent between sites, with large trees (> 20 cm diameter) showing much higher mortality than smaller stems (Nepstad *et al.* 2007; da Costa *et al.* 2010); overstorey species were also disproportionately affected in Tapajos (Nepstad *et al.* 2007). Stem growth of large trees was consistently higher in control plots compared with the TFE treatment and wood production declined with time since initiation of TFE (Brando *et al.* 2008; da Costa *et al.* 2010). The biomass loss associated with TFE in Caxuianã was 5.4 Mg C ha^{-1} yr^{-1}, amounting to an 18 - 20 % loss over the study period (da Costa *et al.* 2010). In Tapajos, aboveground net primary productivity (including both wood production and litterfall) decreased by an average of 21 % (Brando *et al.* 2008).

Mechanisms of tree mortality were also investigated at the TFE sites. Leaf respiration increased under TFE (Metcalfe *et al.* 2010a) and there is evidence that trees responded to water stress by closing stomata to reduce transpiration (Fisher *et al.* 2006). Closing of stomata, whilst reducing water loss, results in reduced leaf CO_2 concentrations which would reduce carbon assimilation. Together, this suggests carbon starvation may be one mechanism driving the drought-induced mortality, as carbon expenditure may have been higher than GPP (Metcalfe *et al.* 2010b). Hydraulic failure through processes such as xylem cavitation, rupture of the water column due to vapourisation of water under tension (Field & Holbrook 1989), may also be a cause of drought-induced mortality. A full understanding of the mechanisms of drought-induced mortality have yet to be reached, particularly with regards to the role of phloem transport during drought (McDowell & Sevanto 2010; Sala *et al.* 2010). During drought events, carbon mobilization and transport may also be reduced, limiting the relocation of stored carbon to parts of the plant where it is needed (Sala *et al.* 2010). A recent review of drought-induced mortality proposes a linkage between mechanisms of mortality, with the reduced carbon assimilation limiting the extent to which embolized xylem elements can be refilled as this process requires energy (McDowell *et al.* 2011). The nature of drought-induced mortality in forest trees is currently an active research topic.

Droughts may also affect species composition. Da Costa *et al.* (2010) show that of eight genera for which analysis was possible, three were particularly susceptible to drought-induced mortality. Large canopy trees, and species with low wood density, have also been shown to have higher susceptibility to short-term drought (van Nieuwstadt & Sheil 2005; Nepstad *et al.* 2007; Brando *et al.* 2008; da Costa *et al.* 2010; Phillips *et al.* 2010). Over a longer period with repeated droughts, this trend could result in changes to species and functional composition. Two studies have assessed changes in functional composition over decadal time-scales in single large plots in Central America, and attributed observed changes to drought during the study period (Enquist *et al.* 2011; Feeley *et al.* 2011). Evidence from both a 16.25 ha plot in Costa Rica and a 50 ha plot in Panama show increases in deciduous, compound-leaved, canopy species with high wood density (Enquist *et al.* 2011; Feeley *et al.* 2011). Understanding the long-term effects of drought on the composition and structure of tropical forests remains a key research challenge (Chapter 2).

1.3 Fires

1.3.1 Fire history of tropical forests

Tropical, moist, closed canopy forest is only weakly susceptible to fires, especially those dominated by evergreen species (Uhl *et al.* 1988). This is due to the ability of closed canopy evergreen stands to maintain humidity below the canopy as transpired moisture is trapped (Cochrane 2003). However, charcoal has been found in many tropical forests dating back several millennia suggesting that occasional fire has been a long-term feature of these ecosystems. For example, charcoal was dated to 1000 and 2000 yr BP in Guyana (Hammond & ter Steege 1998) and at similar times in La Selva, Costa Rica (Horn & Sanford 1992). In additional, Sanford *et al.* (1985) found a number of charcoal samples in soils from Venezuela dated to between 250 and 6260 yr BP. The occurrence of these fires coincides with known dry phases (Sanford *et al.* 1985) during which time even closed canopy forests may have become flammable. The presence of charcoal in sediment cores measured up to 7500 yr BP likely indicates fires caused by indigenous populations, which decreased 500 yr BP following the European colonisation of the Americas (Bush *et al.* 2007; Nevle & Bird 2008). The fire return intervals (time between repeated burns at the same site) of 400 - 1560 yr suggested by Sanford *et al.* (1985) are considerably longer than the fire return intervals observed at present. For example, Alencar *et al.* (2011) estimate 82 yr fire return intervals in an area of Eastern Amazon, and Barlow & Peres (2008) observed forest fires affecting the same area three times within 10 years in central Amazon.

1.3.2 Current fire occurrence

Since the strong 1982/83 ENSO drought that affected much of the tropics and led to unintentional understorey forest fires in Africa (Swaine *et al.* 1997) and South East Asia (Goldammer & Seibert 1989), more attention has be made to the occurrence and impacts of fires in tropical forests. Monitoring the occurrence and spatial distribution of damage from understorey fires is challenging. Remote sensing techniques can provide active fire pixels (hot pixels), showing locations where fires occur (e.g. global coverage using

MODIS, Giglio *et al.* 2003 and South American coverage using the Fire Monitoring Project from CPTEC and INPE). However, such hot pixel products can only identify fires in open areas, rather than understorey fires that occur below the forest canopy (Silvestrini *et al.* 2011). An additional problem of hot pixel products is that they do not give an indication of the area burnt. It is possible to derive burnt areas for tropical forests from Landsat images (Alencar *et al.* 2004; 2006; 2011), however the burnt area signature of the vegetation is only detectable within one to two years of the fire occurrence, and therefore many repeated images are needed to assess burnt areas over time (Alencar *et al.* 2004). This is due to regrowth of vegetation following fire disturbance (Alencar *et al.* 2004). As a result, the production of burnt area maps for tropical forest regions has only been carried out for specific regions and over short time periods. Once burnt area maps have been produced they can be used to investigate which variables result in fires. Alencar *et al.* (2004) show that over 10 years in a 338,000 ha area of the Eastern Amazon half of the forest are was burnt; most fires occurred during ENSO years and previously logged or burnt areas were more commonly affected. Fire occurrence was also correlated with fragment size, distance to forest edge, roads and settlements (Alencar *et al.* 2004). A further study has shown that fire spreads further into the interior of forest fragments during ENSO years (Alencar *et al.* 2006). Extensive fires in Amazonia due to the 2005 drought have also been documented (Aragão *et al.* 2007).

Clear links have been made between fire occurrence, strong droughts and human impacts on tropical forests. The edges of fragmented forests have been shown to experience increased tree mortality, increased canopy openness, increased litterfall and hotter, drier microclimates (Kapos 1989; Laurance *et al.* 1998; Sizer *et al.* 2000). These conditions of higher dead biomass on the forest floor and hot, dry microclimates result in increased forest flammability due to an abundance of highly flammable fuels (Laurance 2006). Selective logging of forests also has a similar impact resulting in increased flammability due to opening of the canopy and debris produced from both the logged trees and other trees killed during the extraction process (Uhl & Buschbacher 1985; Holdsworth & Uhl 1997). Ignition sources for understorey fires typically come from slash and burn deforestation fires and agricultural management fires (Uhl & Buschbacher 1985; Laurance 2006). Areas already of increased flammability such as along fragment edges and logged areas are also more likely to be close to such ignition sources than undisturbed forests. Under appropriate climatic conditions such as particularly severe dry seasons these forests can burn, and if conditions are anomalously harsh even undisturbed forests may burn (Barlow & Peres 2006).

These results can then be used in modelling exercises to predict future fire occurrence. Silvestrini *et al.* (2011) produced a model of future fire regimes in the Amazon parameterised using hot pixel data. Vapour pressure deficit and various spatial land use variables were used to estimate the current probability of fire occurrence, and these models were projected to 2050 using future climate change and land use scenarios. The results show that although both future deforestation and climate change may independently lead to increased fire occurrence, the synergy between the two will lead to particularly large increases in the future, resulting in a 50 % increase in fire occurrence by 2050. Soares-Filho *et al.* (2012) developed a process-based understorey fire model to predict forest fire ignitions and fire spread coupled to a vegetation model to assess long-term carbon balance in the Xingu area of Amazonia. Findings from this study suggest that, although climate change alone will result in an increase in the percentage of forest burnt, forest fragmentation had the largest impact on future fires. As patterns of deforestation and degradation as well as climate change are likely to affect all tropical areas in the future and therefore fire occurrence in tropical forests is likely to rise, providing data to calibrate these models is of high importance.

1.3.3 Impacts of fires on tropical forests

Understorey fires tend only to consume dry leaf litter on the forest floor (Cochrane *et al.* 1999) but can have large impacts on forests and result in highly elevated tree mortality. However, mortality rates, typically measured within 3 years of the fire event, show wide variation. A review by Barlow & Peres (2006) showed that the percentage of trees dying due to fire can vary between 8 and 90 %. This variation can be attributed to a number of sources which are themselves interlinked. Forests in different areas may have had different historical exposure to fires, and places with higher exposure may have developed a more fire resistant floristic composition (Barlow & Peres 2006). For example, fires in core Amazon forest regions show higher tree mortality (36 - 64 %) than forests located at the fringes of the Amazon (8 - 23 %) (Barlow & Peres 2006). Fire intensity, commonly measured using the presence and heights of fire scars on tree boles, is also a strong predictor of tree mortality (Cochrane & Schulze 1999; Barlow *et al.* 2003a; Barlow & Peres 2004; Balch *et al.* 2008; Brando *et al.* 2012). Even within a single study area there can be considerable variation in fire intensity (Cochrane & Schulze 1999) which may be due to spatial heterogeneity in microclimate, fuel load or disturbance history. Forests that have been recently disturbed (e.g. logged forests) are likely to burn more severely with their higher fuel loads and open canopies (Holdsworth & Uhl 1990). Therefore both long-term fire history and recent disturbance history are likely to influence the impact of fires on forests.

The susceptibility of individual trees within a stand also shows heterogeneity, and is linked to tree size and the traits of different tree species. Many studies have shown that small trees show higher post-fire mortality than large trees (Cochrane & Schulze 1999; Pinard *et al.* 1999; van Nieuwstadt & Sheil 2005; Balch *et al.* 2011; Brando *et al.* 2012). This has been linked to the thin bark present on small trees. Bark thickness of tropical forest trees increases as a function of tree diameter and varies among species (Uhl & Kauffman 1990; Pinard & Huffman 1997; van Nieuwstadt & Sheil 2005; Paine *et al.* 2010; Brando *et al.* 2012). Trees with thinner bark show higher cambium temperatures under experimental fires than thicker barked trees (Uhl & Kauffman 1990; Pinard & Huffman 1997; Brando *et al.* 2012); heat transfer rate and maximum cambium temperature decrease exponentially with increasing bark thickness (Uhl & Kauffman 1990; Pinard & Huffman 1997; Brando *et al.* 2012). However, the presence of water within bark is also important in determining heat transfer through bark as it limits the cambium temperature to a maximum of 100°C (Brando *et al.* 2012). Small trees may also be at higher risk of fire-induced mortality because their stems are more likely to be burnt all around their circumference (Gutsell & Johnson 1996; Balch *et al.* 2011). Other factors may also be important. For example, trees with buttresses have been shown to have thinner bark for their size than other species, with bark particularly thin at the base of the bole where trees are at risk of burning (Barlow *et al.* 2003a). In addition, larger trees and those with buttresses have greater loads of fine fuels at their bases which may lead to more intense burning (Barlow *et al.* 2003a). Wood density has also been found to correlate with fire-induced mortality, with denser wooded species showing higher survival rates (Brando *et al.* 2012).

As there is variation in traits such as bark thickness among species, certain species also have a higher chance of survival which may lead to altered species composition between the pre-fire composition and those trees which survive. Furthermore, species typically restricted to the understorey with smaller maximum sizes may suffer increased mortality. Differences in fire-induced mortality between species have been found in some studies (van Nieuwstadt & Sheil 2005; Balch *et al.* 2011). For example, assessing species abundance two years after fires compared with pre-fire abundances in Borneo, Slik *et al.* (2010) found that species which declined in abundance had thin bark, population structures dominated by small trees, short seed dormancy and hillside or ridge habitat preference. These results match the hypotheses that species most vulnerable to fire-induced mortality will have thin bark and smaller individuals. Species with short seed dormancies would be less likely to regenerate post-fire, and hillside and ridge habitats may have lower soil moisture and therefore experienced more intense fires (Slik *et al.* 2010). These results show that fire-induced mortality can generate differences in forest composition after fires.

Not all impacts of fires occur immediately following the fire event. Assessing mortality in the first three years following fires, it has been shown that elevated mortality still occurs one or two years after the fire (Holdsworth & Uhl 1997; Cochrane *et al.* 1999; Barlow *et al.* 2003b; Brando *et al.* 2012). Barlow *et al.* (2003b) show that in the years post-fire the mortality of large as well as small trees can be elevated, suggesting that large trees may have some susceptibility to time-lagged fire-induced mortality.

After an initial fire, the forest becomes more susceptible to subsequent fires which tend to be more severe (Cochrane *et al.* 1999). This is because dead trees provide more fuel on the forest floor (Cochrane & Laurance 2002) which is then dried out extensively as the canopy is more open (Cochrane & Schulze 1999). Grasses and small vines tend to invade post fire, adding more potential fuel (Cochrane *et al.* 1999; Pinard *et al.* 1999). This allows forests to burn under conditions where a primary forest normally would not. For example, of unburnt logged forests in Para, Brazil, only 4% were expected to become flammable with 16 rainless days, whereas 51% of lightly burnt logged forests and almost 100% of severely burnt forests were expected to become flammable (Cochrane & Schulze 1999). The effects of subsequent burns are more severe than initial fires; Barlow & Peres (2008) describe a cascade of changes in species composition with unburnt, once burnt, twice burnt and thrice burnt forests composed of a series of different groups of species. Stem density of all size classes also decreased with subsequent burns (Barlow & Peres 2008). Living biomass is heavily reduced with increasingly severe fire histories (Cochrane & Schulze 1999) and the survival advantage of thick barked larger trees in initial fires may be lost with the increased severity of repeated fires (Cochrane & Schulze 1999; Cochrane 2001). However, Balch *et al.* (2008) found that fire intensity and spread may be limited by fuel availability during repeated experimental burns.

Although the short-term impacts of forest fires are relatively clear, the long-term impacts of fires are not well known, with few studies assessing recovery after fires over more than a few years. In the first years post-fire, growth and recruitment of seedlings and saplings is increased in burnt forests compared with unburnt sites (Swaine *et al.* 1997; Cleary & Priadjati 2005; Gould *et al.* 2002). Given seven years of regeneration, stems > 5 cm diameter increased compared with 1.5 years post-fire, but biomass of stems > 10 cm diameter declined (Slik *et al.* 2008). Nine years after fires in the Brazilian Amazon stem density in the 10 - 20 cm diameter size class was similar to that of adjacent unburnt forests, but other size classes showed little recovery (Barlow & Peres 2008). After 15 years stem density of trees ≥ 10 cm diameter reached the densities of unburnt forests in sites in Borneo (Slik *et al.* 2002; Barlow & Peres 2008; Slik *et al.* 2008). However, the regenerating stems in these studies are typically made up of early successional pioneer species, and floristic composition remains significantly altered (Slik *et al.* 2002). These results suggest that forest structure can regenerate within a few decades of fire events, but composition requires longer to recover. The decadal-scale recovery of forest structure and functional composition in Ghanaian tropical forests will be examined in Chapter 3 of this thesis, utilising plots established in previously burnt forests.

1.4 Lianas

1.4.1 Background

Lianas are woody vines commonly found in tropical and some temperate forests (Schnitzer & Bongers 2002), with maximum biomass and diversity in tropical forests (Gentry 1991). Lianas germinate on the forest floor and use the support of trees to reach the canopy (Putz & Holbrook 1991). Lianas can enter a tree either by growing up the trunk or moving laterally from the crown of an adjacent tree, and they can grow laterally along the ground and re-root away from the original rooting point (Schnitzer and Carson 2001, Gerwing *et al.* 2006). As lianas use trees for structural support they can put more of their biomass into leaf area and reproduction, giving them a high leaf area:stem biomass ratio (Putz 1983); as a functional group their leaves make up a large proportion of the canopy (up to 40%; Hegarty & Caballé 1991) despite contributing just 5% of total aboveground biomass (DeWalt & Chave 2004; van der Heijden & Phillips 2008). They make up to 15% to 25% of stems of woody plants in sample plots (Schnitzer & Bongers 2002) and in Neotropical and Southeast Asian forests 40-60% of trees ≥ 10 cm diameter carry a liana (Laurance *et al.* 2001).

Different liana species have different mechanisms for climbing trees: the may be twiners, tendril climbers, root climbers or hook climbers (Putz & Holbrook 1991; Padaki & Parthasarathy 2000). Twiners can have either stems or lateral leaf-bearing branches which can twist in a helical manner to attach firmly to supports (Putz & Holbrook 1991; Padaki & Parthasarathy 2000). Tendril climbers have specific organs which can twist around supports but differ from twiners in that the tendril organs have a sensitivity to contact with supports which elicits a coiling response. Hook climbers posses hooks on stems, leaves or modified flowers. They do not carry out searching movements, but hooks in contact with a support become stronger (Putz & Holbrook 1991). Root climbers utilise adventitious roots to attach to the tree surface (Padaki & Parthasarathy 2000). Lianas of different climbing mechanism have the ability to enter hosts of different sizes. For example, tendril climbers were found to only climb trees of maximum diameter of approximately 8 cm, whereas branch twiners could climb trees up to a maximum of 16 - 24 cm diameter in Panamanian and Malaysian forests (Putz 1984a, Putz & Chai 1987, Putz & Holbrook 1991). Root climbers can attach to irregularities in bark and hence can potentially climb trees of all sizes (Darwin 1867; Jiménez-Castillo & Lusk 2009).

1.4.2 Impacts of lianas on host trees

Lianas depend on host trees for structural support and as such are parasites on the tree. Putz (1984a) lists a number of ways lianas can negatively impact their hosts such as mechanical abrasion, passive strangulation, damage by wind and increasing accessibility of trees to potentially damaging animals. As a result, lianas increase host-tree mortality. Using data from 13, 1 ha Amazonian plots Phillips *et al.* (2002) found that liana infestation increased tree mortality by 39.6 ± 31.3 % compared with uninfested trees. Large trees (≥ 50 cm diameter) with liana infestations had a basal area mortality rate three times higher than uninfested large trees in Western Amazonian forests (Phillips *et al.* 2005). Similarly, on Barro Colorado Island (BCI) twice as many heavily infested trees died over an 11 year study period compared to trees free from lianas (Ingwell *et al.* 2010). Lianas are also known to decrease tree growth rates. Clark & Clark (1990) found that both the basal area of and extent of tree crown occupied by lianas and hemiepiphytes correlated negatively with annual tree diameter growth, whilst van der Heijden & Phillips (2009a) show that trees ≥ 10 cm diameter heavily competing with lianas have reduced diameter growth rates (32 - 82 % reduction) compared with uninfested trees. Lianas also reduce host tree seed production (Nabe-Nielsen *et al.* 2009).

Lianas have a negative impact on tree growth and mortality because they compete with host trees for resources (Schnitzer & Bongers 2002). Aboveground, leaves of lianas are in close proximity to host leaves and therefore compete with them for light (Clark & Clark 1990), although not all liana species compete with their hosts in this way (Ichihashi & Tateno 2011) and lianas of differing climbing strategies may differ in the amount they shade their hosts (Llorens & Leishman 2008). Lianas also posses extensive root and efficient vascular systems (Ewers *et al.* 1991; Schnitzer 2005) making them efficient belowground competitors.

The relative importance of aboveground and belowground competition between lianas and trees has been investigated with varying results. In an experiment on tree saplings in Cote D'Ivoire, Schnitzer *et al.* (2005) found that belowground competition had a larger impact on sapling biomass than aboveground competition, however saplings carrying lianas in their crowns did show altered allocation patterns suggesting mechanical stress. A similar result was found by Toledo-Aceves & Swaine (2008) from a shade-house experiment in Ghana: below ground competition had a larger impact on seedling growth than above ground competition. Liana removal from adult trees increased tree water potential during the dry season in Bolivia, showing effective competition for water by lianas (Pérez-Salicrup & Barker 2000). However, the result was not found when a different tree species was assessed (Barker & Perez-Salicrup 2000). In a temperate habitat, belowground competition was again found to be more important than aboveground competition (Dillenberg *et al.* 1993). In contrast, van der Heijden & Phillips (2009a) suggested that aboveground competition was more important than belowground competition in reducing tree growth of Peruvian trees, although this was purely an observational study. Experiments also show that the importance of aboveground and belowground competition may vary depending on irradiance, with aboveground competition more important under low light conditions and belowground competition more important under high light conditions the for the growth of tree seedlings (Chen *et al.* 2008). The importance of belowground and aboveground competition remains unclear, and may vary between species. In contrast to these studies of competition, it has also been suggested that as lianas have high turnover of their high nutrient and abundant leaves (Zhu & Cao 2010), they may benefit trees by providing additional nutrients to the soil, especially those lianas that root away from their position in the canopy (Tang *et al.* 2012).

Lianas do not infest trees in a random manner (Putz 1984a). Trees with large diameters have been found to carry larger infestations of lianas than smaller trees (Clark & Clark 1990; Pérez-Salicrup *et al.* 2001; Pérez-Salicrup & de Meijere 2005; Nesheim & Økland 2007), though Carsten *et al.* (2002) found that infestation with lianas of different climbing mechanisms gave different relationships with host diameter. Addo-Fordjour *et al.* (2009) found no significant relationship between tree diameter and liana load in Ghana. Larger trees may be likely to carry more lianas as they may have been exposed to the risk of infestation for a longer time than smaller trees, and infestation by one liana can provide an access route for other lianas (Putz & Chai 1987; Campbell & Newbery 1993; Pérez-Salicrup *et al.* 2001). Once a tree has acquired one liana, it is likely to acquire more. For example, liana infestation is commonly found to be aggregated in certain trees, with some having higher and some lower number of lianas than would be expected if infestation occurred at random (Campbell & Newbery 1993; Putz 1984a; Pérez -Salicrup *et al.* 2001). Factors that have been found to reduce liana infestation include high branch-free bole height (Balfour & Bond 1993; Campbell & Newbery 1993; van der Heijden *et al.* 2008), long leaves (Putz 1984b; van der Heijden *et al.* 2008), branch shedding (Campbell & Newbery 1993; Carse *et al.* 2000) and flexible trunks (Putz 1984b). High branch-free bole height may prevent lianas from having access to the canopy, whilst large leaves, when shed, may dislodge lianas present in the tree, as would branch shedding and the movement of flexible trunks. In the case of root-climbing lianas, bark characteristics are also important (Talley *et al.* 1996). Lower growth rates have been found to correlate with increased liana infestation (Clark & Clark 1990) which is most likely due to a combination of the fact that lianas reduce tree growth (van der Heijden & Phillips 2009a) and that traits that reduce liana infestation such as high branch-free bole height and long leaves are correlated with faster growing species (van der Heijden *et al.* 2008). Such traits are species-specific which is consistent with some species carrying more or less lianas than expected by chance (Campbell & Newbery

1993; Carse *et al.* 2000; Carsten *et al.* 2002; Nesheim & Økland 2007; van der Heijden *et al.* 2008; Jiménez-Castillo & Lusk 2009). If particular species are infested by lianas more than others, and the presence of lianas has a negative impact on host trees, it is likely that lianas may impact patterns of tree species composition in tropical forests.

1.4.3 Liana spatial distribution

Low rainfall and high seasonality, disturbance, forest structure and soil fertility have all been proposed as spatial drivers of liana abundance (Putz 1984a; Schnitzer & Bongers 2002). In particular, Schnitzer (2005) provides a compelling argument that liana distribution is driven globally by precipitation and dry season length. This hypothesis is driven by evidence that lianas are better adapted to cope with water stress giving them a competitive advantage over trees. The structure of lianas with long, narrow stems and large leaf area requires a larger amount of water to be transported through a much smaller stem cross-sectional area than for trees. As such, lianas have a different xylem physiology compared to trees, with larger vessel elements, lower sapwood density and higher hydraulic conductivity (Carlquist 1991; Ewers *et al.* 1991; Tyree & Ewers 1991; Ewers *et al.* 1997; Zhu & Cao 2009). To prevent embolism, lianas have deep and expansive root systems to reach deep water sources during seasonal droughts (Restom & Nepstad 2004; Andrade *et al.* 2005). These physiological adaptations enable lianas to remain photosynthetically active during seasonal droughts when trees may lose their leaves; this gives lianas an advantage of less competition with trees during the period when irradiance is highest (Putz & Windsor 1987; Schnitzer 2005). To support this, Cai *et al.* (2009) present clear evidence that lianas fix more carbon than trees, particularly during the dry season.

A number of studies have tested the hypothesis that rainfall and seasonality drive liana distribution. Using the pantropical Gentry dataset of 0.1 ha plots, Schnitzer (2005) found a significant relationship between increased precipitation and liana density (precipitation range 500 - 7,500 mm yr-1). Using a pantropical dataset DeWalt *et al.* (2010) also find evidence in support of the relationship between low rainfall (range 860 -

7,250 mm yr-1), high seasonality (range 0 - 7 months < 100 mm) and liana abundance. Assessing a large dataset along a shorter rainfall gradient (1113 - 2198 mm yr-1) in Bolivia, Toledo (2011) find that the percentage of trees infested with lianas decreased with increasing rainfall, also supporting the results of Schnitzer (2005) and Dewalt *et al.* (2010). Swaine & Grace (2007) assessed a similar precipitation gradient (1000 - 2000 mm yr-1) in Ghana and found a significant relationship between decreasing rainfall and increasing liana species as a proportion of tree, herb and liana species, however it does not directly address liana abundance. In contrast, using only the Neotropical data from the Gentry dataset van der Heijden & Phillips (2008) found no relationship between precipitation or rainfall seasonality and liana abundance (precipitation range 500 - 9,000 mm yr-1, dry season length range 0 - 11 months < 100 mm). Testing relationships between rainfall, dry season length and liana species richness (after accounting for liana abundance) using the same Neotropical dataset, van der Heijden & Phillips (2008) found that liana species richness increased with decreasing dry season length. The majority of available evidence suggests liana abundance does increases in areas of lower rainfall and greater seasonality, but not all studies support this.

Disturbances at various scales have also been shown to be drivers of liana abundance. At small scales liana abundance has been related to treefall gaps. Schnitzer & Carson (2001) investigated species diversity in treefall gaps on Barro Colorado Island and discovered that liana diversity, both per unit area and per individual, was higher in treefall gaps than in closed canopy forest areas. Abundance was also greater at gap sites. The increase in lianas in treefall gaps may be due to lianas having four methods of gap colonization (from the seed bank, advance regeneration, growing laterally into a new gap or surviving when a tree in which they are resident falls and regrowing in the gap), whereas trees can only colonize from the seed bank or advance regeneration (Schnitzer & Carson 2001). The presence of small tree stems within tree fall gaps may also increase liana abundance as it provides a trellis upon which small lianas can climb (Putz 1984a). Some treefall gaps may even become dominated by lianas at the expense of trees and persist in this state for many years (Schnitzer *et al.* 2000; Foster *et al.* 2008). Within old growth forest patches of different tree heights (< 3, 3 - 15 m, 15 - 25 m and > 25 m), liana density and basal area decreased with forest height, again showing their affinity for gaps and early successional stands (Gerwing & Farias 2000). Liana species richness and basal area were found to increase with plot-level tree wood density (a proxy for forest disturbance, van der Heijden & Phillips 2008; van der Heijden & Phillips 2009b). At larger scales of disturbance, studies assessing liana abundance along gradients of secondary forest age have also found significant trends. DeWalt *et al.* (2000) assessed liana abundance along a chronosequence of secondary forests 20, 40, 70, and 100 years after abandonment and old growth forests, and reported increased liana abundance in younger Panamanian forests; however liana biomass increased with forest age. Composition of lianas and climbing strategy also varied across stands of different ages, suggesting different species may have different requirements with regard to support structures. Similar results have been found in other secondary forests of varying ages; Yuan *et al.* (2009) show liana abundance was higher in younger sub-tropical forests, and along the chronosequence liana species composition and climbing strategy varied, whilst Madeira *et al.* (2009) found the highest liana abundance in seasonally dry tropical forests of intermediate successional stage. Liana diversity was reduced in Malaysian secondary forests, but abundance remained was similar in primary and secondary forests whilst liana basal area was considerably higher in primary forest (Addo-Fordjour *et al. in press*). Forest fragmentation can also alter forest structure and dynamics. Laurance *et al.* (2001) studied the effects of forest edges on liana spatial distribution and found that the abundance of lianas increased significantly within 100 m of edges compared to the forest interior. However, the relationship was complex as plots > 1000 m from the edge also had high liana abundances, and had a higher proportion of lianas > 10 cm diameter (Laurance *et al.* 2001).

Differences in forest structure, and therefore host availability, may contribute to the patterns found along secondary forest chronosequences and in disturbed areas. Relationships between liana abundance and forest structure are also likely to be important in old growth forests. In fragmented forests, liana abundance decreased with tree biomass (Laurance *et al.* 2001). In contrast, large lianas (≥ 10 cm diameter) increased with large tree basal area in forest plots in Peru (Phillips *et al.* 2005). In Yasuni National

Park, Ecuador, liana abundance was positively correlated to small tree density (1 - 10 cm diameter), but not to density of trees ≥ 10 cm diameter (Nabe-Nielsen 2001). Liana abundance was correlated with a vegetation index reflecting tree size class distribution in Central Amazonia, corresponding to increased liana density with more smaller trees (Nogueira *et al.* 2011). Across the Neotropics, liana density was found to be related to density of trees ≥ 10 cm diameter, and liana basal area was related to basal area of trees ≥ 10 cm diameter (van der Heijden & Phillips 2008). These results show a strong link between forest structure and liana abundance.

Liana distribution may also be related to soil fertility; Gentry (1991) found low abundance in very low fertility sites and high abundance in very fertile sites. Lianas may increase with soil fertility due to the high nutrient demand of their nutrient rich, extensive and high turnover foliage (Zhu & Cao 2010). However, relationships between soil fertility and liana abundance are not always found. Laurance *et al.* (2001) show higher liana biomass correlates with increased levels of P, clay, pH and exchangeable bases, and decreased sand content in 1 ha plots across a landscape of the central Amazon. In contrast van der Heijden & Phillips (2008) found no relationships between soil variables and liana density and only a weak effect of Cu concentration on liana basal area from a dataset with samples from across the Neotropics. The literature also presents contrasting relationships between soil sand content and liana abundance. Across an environmental gradient in Bolivia, Toledo (2011) found liana abundance increased with soil sand content, whilst Nogueira *et al.* (2011) found liana density decreased with sand content over a 64 km^2 are of the Central Amazon. Further work is required to fully comprehend the associations between soil properties and liana distribution.

1.4.4 Recent increases in liana abundance

Recent work on the dynamics of lianas in undisturbed Neotropical forests shows an increase in abundance over time (Phillips *et al.* 2002; Wright *et al.* 2004; Wright & Calderon 2006; Ingwell *et al.* 2010). Phillips *et al.* (2002) used data from 47, one ha plots in the Neotropics with information on lianas ≥ 10 cm diameter and found that both the growth and mortality of lianas were increasing, with the increase in growth being greater than the increase in mortality. Both density and basal area increased between 1981 and 2001. The biomass of trees in the Amazon also increased over the same time period (Baker *et al.* 2004a) but the increase in lianas was much more rapid, leading to a much higher liana basal area to tree basal area ratio; the dominance of lianas increased by 1.7 - 4.6 % yr^{-1} (Phillips *et al.* 2002). This large-scale study is supported at a local scale by a number of studies from Barro Colorado Island, Panama. Wright *et al.* (2004) studied the changes in liana leaf litter, seed production and seedling density for 17, 15 and 9 years respectively in a 50 ha plot. The results from the leaf litter study indictated that the proportional contribution of lianas to the leaf litter increasing from 10.9% to 17.1% between 1986 and 2002. Similarly, between 1987 and 2003, flower production increased by 4.1 % yr-1 (Wright & Calderon 2006). The percentage of trees ≥ 20 cm diameter infested on Barro Colorado Island has also increased, from 43 - 47 % in 1980 (Putz 1984a) to 73.6 % in 2007 (Ingwell *et al.* 2010). However, not all studies support the trend of increased liana abundance. A study from Gabon shows a 20 % decline in liana density and no change in liana basal area between 1979 and 1992 (Caballé & Martin 2001), though this is based only on a small 1.6 ha site. In a larger study of two, 10 ha plots in the Democratic Republic of Congo, Ewango (2010) found a 33.5 % decrease in liana stem density between 1994 and 2007. Further study, particularly outside of the Neotropics, is required to assess the generality of these patterns.

As described above lianas have a negative impact on the trees they grow in and an increase in lianas could result in increased in tree mortality. This could result in positive feedbacks on liana abundance as increased tree mortality may lead to increased presence of treefall gaps, which would then lead to increase in liana abundance (Phillips & Gentry 1994; Gerwing & Farias 2000; Schnitzer & Carson 2001). These effects could reduce the carbon storage and sequestration capacity of forests. It is also possible for lianas to delay successional processes (Schnitzer *et al.* 2000; Foster *et al.* 2008) and become dominant over other plant types resulting in “liana forests” with considerably lower biomass (Gerwing & Farias 2000). There is also evidence that the size of such liana dense forest patches have increased in recent years (Foster *et al.* 2008). Disturbance may also lead to positive feedbacks where opening of the canopy increases liana abundance and the presence of lianas increases the susceptibility of trees to wind and fire damage as well as suppressing successional processes at forest edges (Laurance *et al.* 2001). Increases in the dominance of lianas would give a selective advantage to those tree species with characteristics that reduce liana infestation (e.g. long leaves, low density wood, fast growth rates; Putz 1984b; Balfour & Bond 1993; Campbell & Newbery 1993; Carse *et al.* 2000; Pérez-Salicrup *et al.* 2001; van der Hiejden *et al.* 2008). These trees tend to have lower carbon storage capacity so in addition to lowering carbon storage by increasing tree mortality, selection for more liana-resistant trees could also lower tropical forest carbon stocks; van der Heijden *et al.* (2008) calculated that trees without lianas tended to store 25% less carbon than those with lianas.

1.4.5 Drivers of increased liana abundance

The observed increase in abundance and basal area of lianas over time in Neotropical sites has led to a vigorous debate about the possible causes. Phillips *et al.* (2002) suggest that the increase in lianas is due to increases in atmospheric CO_2. The effects of CO_2 enrichment has been examined by Granados & Körner (2002) in a laboratory setting looking at the changes in growth of three liana species at different light levels (photon flux density 42 and 87 μmol m^{-2} s^{-1}) and CO_2 concentrations (280, 420, 560 and 700 ppm). The results show that under all conditions liana biomass increased with increasing CO_2. For two of the three species investigated the increase in growth was a linear response to CO_2. In contrast, the third species initially increased in biomass but CO_2 levels above 560 ppm resulted in a slight decline in growth. A key finding of this study is that the relative growth increase of lianas was higher in low light than in high light environments (though total growth was higher in high light). The implication of this finding is that lianas in low light, such as those in the understorey, may get a greater boost in growth from increased CO_2 than those in high light, such as those in the canopy. This pattern might increase the ability of lianas to reach and dominate the canopy. It also may increase the potential range of microenvironments lianas can persist in, as they may be able to grow under condition where previously they may not have been able to (Granados & Körner 2002). It was also noted by Granados & Körner (2002) that shoot rigidity (but not stem length) was increased under increased CO_2. This might enhance survivorship of shoots and success of the liana. Similar increased growth responses to elevated CO_2 were found by Condon *et al.* (1992); under 1000 ppm CO_2 growth increased by 5.5 and 7.1 times for two liana species compared to plants grown at 350 ppm CO_2.

An alternative theory is provided by Wright *et al.* (2007) who propose that bushmeat hunting has an effect on plant species composition as hunting causes removal of some seed dispersers and therefore have a detrimental impact on plant species dispersed by hunted animals; as lianas are commonly dispersed by wind they may be exposed to reduced competition from animal dispersed species. The results presented by Wright *et al.* (2007) show an increase in the abundance of liana seedlings in sites experiencing high levels of hunting; however, the effect on adult population was not assessed. This mechanism of increasing liana abundance would only be possible at sites that are under influence of hunting and is therefore unlikely to be responsible for the increases across multiple sites across the Neotropics.

A third potential explanation is that the observed increase in tree turnover (Phillips & Gentry 1994; Phillips *et al.* 2004) may increase liana abundance by increasing the number of gaps which they can exploit (Phillips *et al.* 2002; Schnitzer & Bongers 2011). Similarly, anthropogenic disturbance in tropical regions may also favour liana abundance (Schnitzer & Bongers 2011).

Furthermore, Schnitzer & Bongers (2011) suggest that as lianas may increase with greater water stress (Schnitzer 2005), climate changes such as increased temperatures and changes to precipitation regimes resulting in increased evapotranspiration may have lead to this trend. The resultant increase in water stress may then increase the competitive ability of lianas over trees. Supporting this, a recent study shows seed germination and shoot biomass of *Ipomoea cairica* (an invasive liana) increased with increased temperature when grown at 22, 26 and 30°C (Wang *et al.* 2011). Given the importance of lianas to forests, it is important to determine the cause of the increase in Neotropical lianas and investigate if it is occurring on other continents. Chapter 4 of this thesis will test whether lianas have increased in abundance in Ghanaian forests and determine the dominant drivers of their spatial distribution across the forest zone.

1.5 Ghanaian forests

1.5.1 Climate and soils

Ghana is located in West Africa bordering Togo, Cote D'Ivoire and Burkina Faso, with a coast line along the Gulf of Guinea (Fig. 1.1). Tropical forests in Ghana extend from the coast northwards to approximately half way up the country, where there is a transition zone to savannah vegetation (Fig. 1.1). The forest is part of the Guinean forests that extend from Sierra Leone in the West to Cameroon in the East and are amongst Conservation International's 25 conservation hotspots due to its high number of endemic plant taxa (2,250 species) and high level of threat with only 10 % of original forest remaining (Myers *et al.* 2000). The Guinean forest region is split by the Dahomey gap from Togo to Nigeria, with savannah vegetation, into Upper and Lower Guinean forests (Fig. 1.1). However, the Dahomey gap was likely to have been forested during the mid-Holocene (Maley 1991).

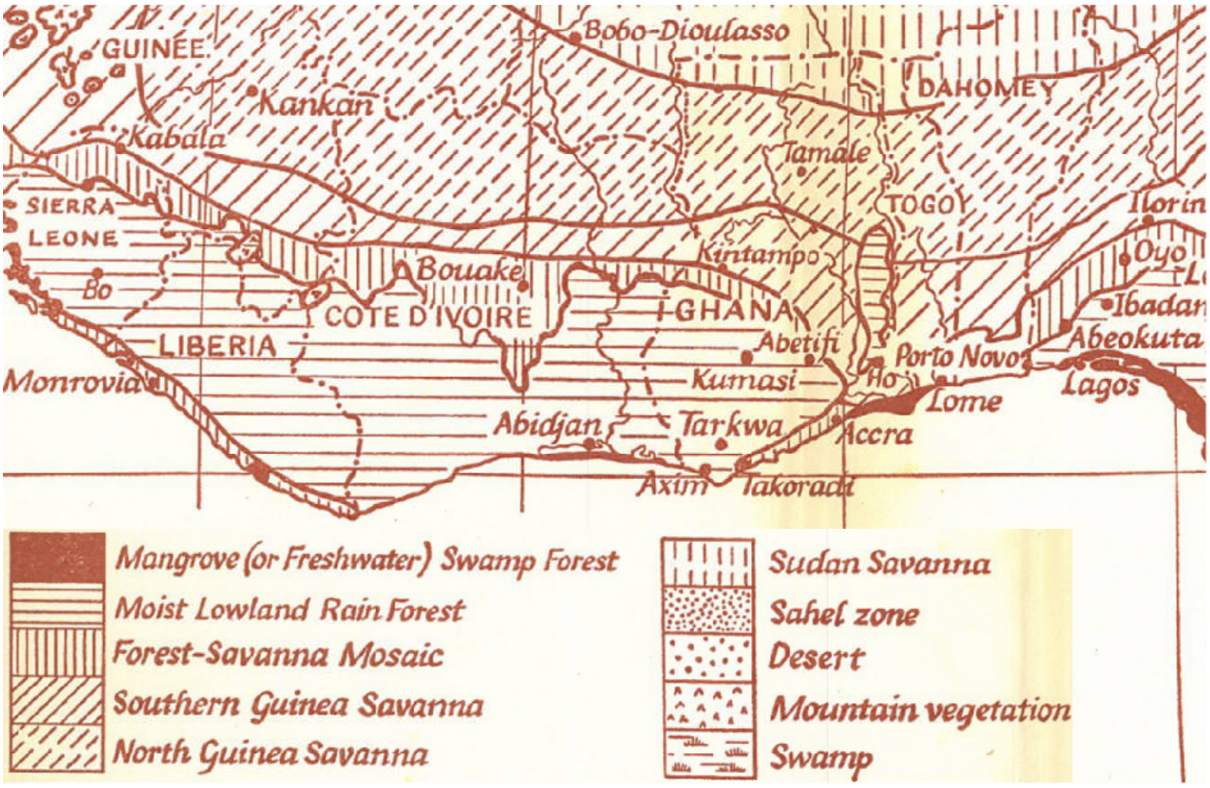

Figure 1.2. Upper Guinea forests and other natural vegetation types of West Africa. (From Nielsen 1965).

Ghana has a strong precipitation gradient with the highest rainfall in the south west (rainfall > 2000 mm yr^{-1}) which decreases to the north and east (Swaine *et al.* 1997). The rainfall gradient is shown in Fig. 1.2a. The higher annual preciptation towards the south west is due to higher rainfall during the wet season, dry season length is similar across the forest zone (Hall & Swaine 1976). Rainfall is bimodal. The major dry season runs from November (or December) to February, a three of four month continuous dry season (months < 100 mm). Four month dry seasons occur in locations with lower annual precipitation. The second dry season occurs in August due to the movement of the Intertropical Convergence Zone (ITCZ). Rainfall in the Ghanaian and Ivorian forest zones is typically lower than in Sierra Leone and Liberia due to their position in the rain shadow of the latter two countries, and due to the parallel angle of the coastlines to the onshore winds (Poorter *et al.* 2004). Areas of high rainfall have lower soil fertility due to the leaching of nutrients (Swaine 1996; Swaine *et al.* 1997), and the effects of climate is thought to override the influence of parent material on forest soil (Hall & Swaine 1981).

The forest zone soils are considered to be heavily weathered latosols (or ferralsols) with low humus and low cation exchange capacity; there are two types, oxisols that are strongly leached, acidic and nutrient poor and less leached, slightly acidic to neutral and less nutrient poor ochrosols (Hall & Swaine 1981).

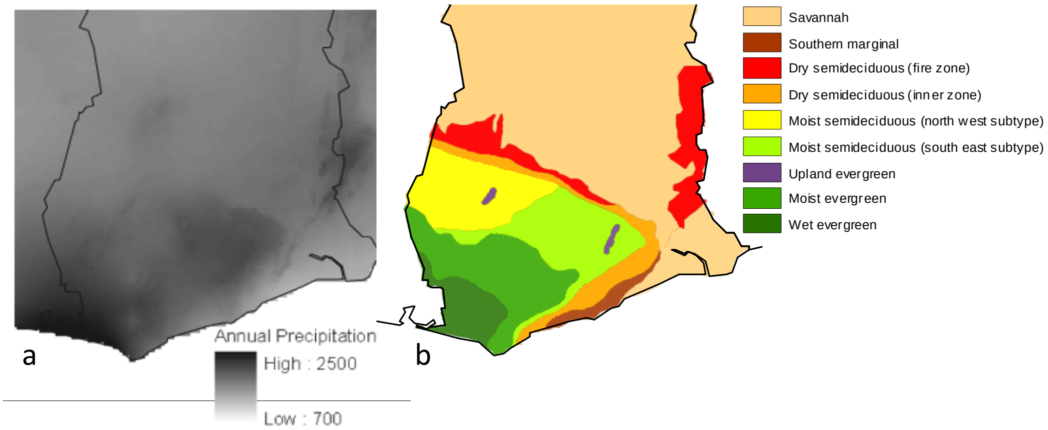

Figure 1.2. Annual precipitation across Ghana based on WorldClim interpolated data (Hijmans *et al.* 2005) (a) and vegetation types based on Hall & Swaine (1976) (b), courtesy of Ghana Forestry Commission.

The climate in Ghana has followed the same trends as the rest of West Africa for the period 1960-1998; temperatures increased by 0.1 - 0.3°C per decade and precipitation decreased by -2 to -12 mm yr^{-1} (Malhi & Wright 2004).

1.5.2 Forest types

The total area of the potential forest zone covers 82,260 km^2 with 16,790 km^2 (20%) in forest reserves (Hall & Swaine 1976). The reserves were set up with aims of watershed protection and climate amelioration and to supply timber as land outside reserves is used for agriculture (Wong 1996). Many of the reserves contain logging concessions (Swaine *et al.* 1997). Hall & Swaine (1976) completed a comprehensive survey of the forest zone to categorise the different closed-canopy forest types found in Ghana. They used a systematic sampling methodology across the forest zone using 155, 25 m x 25 m plots (0.0625 ha) in which all trees > 10 cm diameter were identified and counted. In a separate plotless survey readily identifiable species were counted and in 50m x 50m plots all trees > 10 cm diameter were measured. 1248 plant species were recorded in total and soil characteristics from the 25 m x 25 m plots were also measured.

Using this dataset and ordination techniques (detrended correspondence analysis) Hall & Swaine (1976; 1981) categorise the forest as: wet evergreen, moist evergreen, upland evergreen, moist semi-deciduous, dry semi-deciduous, southern marginal and south-east outlier forest types (Fig. 1.2b). In the evergreen forest types typically 10 - 20 % of canopy species are deciduous, increasing to 30 - 70 % in the semi-deciduous forest types. Moist semi-deciduous is the most extensive forest type. It also contains the tallest trees (50 - 60 m) and half of the economic timber species are at their highest abundance. Species characteristic of this forest type are *Celtis mildbraedii*, *Nesogordonia papaverifera*, *Microdesmis puberula* and *Baphia nitida*. The moist semi-deciduous forest type is further split into two subtypes: the north west and south east subtypes. The boundary between the two subtypes corresponds with the 1500 mm rainfall isohyets, with the north west subtype receiving less precipitation and soils are more fertile and with higher pH than the south east subtype. The north west subtype is particularly well stocked with timber species. On the south west coast and extending inland is the wet evergreen forest type. This forest type receives the most rainfall and has the highest species diversity. Soil fertility is low. Canopy species are shorter than in the moist semi-evergreen forest type, reaching 40 m. However the basal area of the two types is similar. Few timber species are present. Characteristic species are *Cyanometra alata*, *Pentadesma butyracea* and *Heritiera utilis* amongst others. The moist evergreen forest type is intermediate between wet evergreen and moist semi-deciduous, but still has a characteristic composition including *Petersianthus africanus*. It receives rainfall similar to the moist semi-deciduous south east subtype but has lower soil fertility. Canopy tree height is a little taller than the wet evergreen forests at 43 m. To the north and east of the moist semi-deciduous forest type is the dry semi-deciduous type. This forest type contains shorter trees, 30 - 45 m, and few species are confined to it. Characteristic species are *Antiaris toxicaria* and *Triplochiton schleroxylon*. Two subtypes have been characterised, one bordering the moist semi-deciduous forest type (inner zone) and the other bordering the savannah (fire zone). As climate and soils do not vary between the subtypes, fire activity has been implicated in causing the differences. The fire zone subtype has few woody species in the understorey, and the distinguishing features between the species occurring the two subtypes are likely related to fire resistance.

The three other forest types are less extensive. Upland evergreen forest occurs within the moist semi-deciduous forest type on hills 500 - 750 m elevation. Canopy tree height reaches 45 m and the type has the lowest percentage of deciduous species. Tree ferns and epiphytes are common. The southern marginal and south east outlier forest types are the driest and contain the shortest trees, 35 m and 15 m respectively. All forest types, including undisturbed areas, were found to contain a high proportion (about 30%) of climbing species.

Rainfall is thought to be the dominant environmental factor leading the different forest types (Hall & Swaine 1976; 1981). However, as precipitation and variation in soil properties co-vary it is difficult to fully determine which is most important. This has been addressed by Swaine (1996), who found that precipitation was a stronger driver of composition than soil fertility. However, variation within the wet evergreen forest can be attributed to differences in soil fertility. When split into four categories, wet-fertile, wet-infertile, dry-fertile and dry-infertile, species distributions for some species are allied to a particular category, showing that soil factors are important, but secondary to rainfall (Swaine 1996).

Recent studies have used the environmental gradients in Ghana to assess the distributions of plant functional traits. For example, Poorter *et al.* (2008) have shown that both rainfall and disturbance are important for tree maximum size, with larger trees occurring in drier areas and in sites with greater disturbance. Furthermore, they confirm the increase in species diversity with increased precipitation, and also find species diversity decreases with increased disturbance. Maharjan *et al.* (2011) assess the distribution of important timber species and their traits along environmental gradients of Upper Guinean forests including Ghana and found rainfall an important determinant of species distributions. Ordination of plant traits to determine the main plant life-strategies revealed shade-tolerance on the primary axis of variation and drought-tolerance on the second axis of variation. The forests of Ghana have also been used to test for support of the intermediate disturbance hypothesis that species richness will be greatest where there is an intermediate level of disturbance (Bongers *et al.* 2009). The results show support for the hypothesis but only for the dry forest type. These studies show the importance of both the precipitation gradient and local disturbance for community assemblage.

1.5.3 Fire and Drought History

Fire is known to have a strong effect on forest vegetation in Ghana as shown by the inclusion in Hall and Swaine (1976) of a fire zone subtype of dry semi-deciduous forest. It is particularly important at the forest/savannah boundary at the northern edge of the forest zone (Swaine *et al.* 1997). Fires have been known to occur at the forest savannah boundary for some time, but there appears to have been an increase in fire occurrence since the 1970s, with particularly severe fires during the 1982/83 ENSO event. Since then there have been more fires with more serious effects on the forest. During drier years, fires initiated for agricultural land management outside the forest reserve boundaries are more likely to spread into the forest. The effect of positive feedback of fire susceptibility described above (Section 1.3.3) has also been noted. For example, in some areas fire has been followed by the invasion of *Chromolaena odorata* that grows well post-burn but is highly flammable and competes with other forest species (Swaine *et al.* 1997). The invasion of *C. odorata* increases the risk of fire and reduces the capability of the forest to regenerate. This process results in characteristic vegetation (the dry semi-deciduous fire zone vegetation type) with many pioneer species, often including *Elaeis guianensis* (oil palm) and Marantaceae species, a low number of small and medium sized stems and above average abundance of ground flora. In some extreme cases it appears that forest regeneration was completely terminated by fires; there are areas thought to have had full forest cover earlier in the 20th century that are now dominated by *Panicum maximum* grassland. This has happened in areas with sandy shallow soils but relatively high rainfall, the southern marginal forest type. The increases in fire may also be associated with increased temperatures and greater agriculture. Trends such as this may cause forest to convert to savannah vegetation. However, this process is would require the invasion of savannah species and composition to some form of degraded forest may be more likely (Swaine 1992; Swaine *et al.* 1997).

As well as the strong ENSO event of 1982/83 which resulted in forest fires, the area has been affected by a long-term drought. Data presented by Malhi & Wright (2004) shows that between 1960 and 1998 precipitation in West Africa decreased by 4 % decade^{-1}. This is the strongest precipitation decline of all tropical forest regions (Malhi & Wright 2004). The drought in forested West Africa is paralleled by the Sahel drought to the north which had a significant human impact (Nicholson *et al.* 2000). Looking specifically at Ghana and using data from the Ghana Meteorological Agency, Owusu & Waylen (2009) assessed differences in rainfall between the periods 1950 - 1970 and 1980 - 2000. They found a 10 - 30 % decrease in precipitation for the forest zone of Ghana between the two time periods. The drought has been attributed to a southward shift in the warmest Atlantic seas surface temperatures and the ITCZ, and warming of the Indian Ocean (Dai 2011). Analysis of a sediment core from Lake Bosumtwi, located in the Ghanaian forest zone, confirms the strong relationship between sea surface temperatures and West African drought (Shanahan *et al.* 2009). Furthermore, by assessing 3000 years of climate variability using the Bosumtwi core, it has been found that the drought occurs cyclically on a decadal to centennial time scale, with a particularly strong 40 year cycle (Shanahan *et al.* 2009). The drought since the 1970s in West Africa is therefore part of long-term cycle, and the forest zone of Ghana will have experienced similar droughts in the past.

1.5.4 Plot network

The programme of permanent sample plots (PSPs) in Ghana was initiated in 1969 with the aim of studying the growth of economically important species. Two, 1 ha square plots were selected in every square mile of reserved forest. These plots were split into 25 quadrats for easier enumeration. With the emphasis on timber species the "leading desirable" concept was used to guide the inventories and in each quadrat only the two trees of most economic importance were measured. This method was not suitable for studies of forest dynamics so the Forest Inventory and Management Project overhauled the PSP network in 1988, increasing the number of plots to 600 with the existing plots making up one third of the total (Table 1.1). Between 10 and 20 plots were set up in each forest management unit (about 50,000 ha). (Affum-Baffoe 1996).

Table 1.1. Area and number of plots for each forest classification. (Affum-Baffoe 1996).

Forest Type	Reserve Area (km²)	Number of PSPs
Wet evergreen	1006	50
Moist evergreen	4361	160
Moist semi-deciduous SE	2290	82
Moist semi-deciduous NW	4602	228
Upland evergreen	259	10
Dry semi-deciduous	1991	60
Wet evergreen/moist evergreen	472	10
Other	1360	0
Total	16341	600

Plot establishment was completed by 1994 and remeasurement began in 1995. A 5 year census period was planned. Trees with large buttresses were measured using a relascope and callipers were used if climbers could not be moved away from the stem. The point of measurement was marked with red paint around one third of the bole. Trees were numbered using aluminium tags nailed to the tree below the point of measurement. For each stem ≥ 10 cm diameter, the species, diameter, crown position, crown form and climber status was recorded. The latter three measurements are made on a 5 point scale (Table 1.2).

Table 1.2. Measurement scales of crown position, crown form and climbers used in PSP inventories in Ghana. (Affum-Baffoe 1999).

Crown position	
1	Crown plan entirely shaded vertically and laterally.
2	Crown plan entirely shaded vertically but exposed to some direct side light due to gap or edge or overhead canopy.
3	Crown plan partly exposed vertically but partly vertically shaded by other crowns.
4	Crown plan fully exposed vertically but adjacent to other crowns of equal or greater height within 90 degree cone.
5	Crown exposed vertically, free from lateral competition.
Crown Form	
1	Degenerating, suppressed, badly damaged or likely to die, no true crown present.
2	Distinctly unsatisfactory, extensive dead bark, strong asymmetry, few branches but probably capable of surviving.
3	Just satisfactory, distinctly asymmetrical or thin, capable of improvement given more room.
4	Nearly ideal, silviculturally satisfactory but some slight defect of symmetry or some dead branch tips.
5	The best size and development generally seen.
Climbers	
0	Free from climbers.
1	Climbers on main stem only.
2	Climbers in crown but main stem free.
3	Climbers on main stem and in crown.
4	Whole crown smothered by climbers and present on main stem.

After analysis of the data from these plots it was discovered that there was a high rate of errors, with only 64 % of data points from 66 PSPs found to be error free (Affum-Baffoe 1996). Errors had derived from plot demarcation (such as trees found outside plot boundaries in subsequent surveys and the removal of tree tags etc by hunters), from enumeration (such as the inaccuracy associated with using 1 cm graduated girth tapes and double measurements being carried out on unbuttressed trees) and errors in data entry and processing. This led to changes in the methodology to reduce inaccuracies, including sequential tree numbering, new forms for censuses featuring the data from the previous census and new equipment such as fibre glass survey tapes and diameter tapes. The number of PSPs was limited to 210 with 40 plots in each forest zone (dry semi-deciduous, moist semi-deciduous NW subtype, moist semi-deciduous SE subtype, moist evergreen and wet evergreen) plus 10 in upland evergreen areas (Affum-Baffoe 1996). Most reserves have a proportion of plots within them measured twice with the second measurements with a 10 cm or more commonly 20 cm diameter minimum size class. More recently, recensuses of selected plots have been carried out in collaboration with international research projects: the African Tropical Forest Observatory Network (AFRITRON) and Tropical Forest Biomes in Transition (TROBIT).

1.6 Thesis aims and objectives

1.6.1 Aims

The broad aim of this thesis is to capitalize on the unique dataset available from Ghanaian forests to investigate the impact of potential global threats to tropical forests. The key questions to be addressed are 1) the impacts of long-term drought on functional composition and forest structure across the forest zone, 2) the long-term regeneration of forest structure and functional composition following understorey fires in moist semi-deciduous forests and 3) the spatial and temporal distribution of lianas.

1.6.2 Objectives

1. Test for impacts of long-term drought on Ghanaian forests.
    - 1.1 Collect data from multiple forest types and compile functional trait data for species occurring in the plots.
    - 1.2 Test if changes in functional traits over the decadal study period match hypothesised changes due to drought or other potential drivers.
    - 1.3 Test if these changes have occurred since the onset of the West African drought using an extended temporal dataset.
    - 1.3 Test if forest structure has altered over the study period.

2. Assess the impacts of past fire events on Ghanaian forests and long-term recovery after burning.
    - 2.1 Locate and remeasure permanent sample plots in burnt and unburnt forest areas within the same forest type.

2.2 Test if contemporary functional composition and forest structure are associated with past fire history.

2.3 Test the extent to which burnt forests have recovered since the fire event.

3. Test whether there have been changes over time in liana abundance and determine the drivers of liana spatial distribution.

3.1 Using a dataset of host tree infestation in plots from multiple forest types, test if lianas have increased in abundance.

3.2 Survey current liana abundance and soils in permanent sample plots.

3.3 Test if climate, forest structure, disturbance or soil characteristics determine liana spatial distribution.

To achieve these objectives, plot data from the Ghana Forestry Commission, AFRITRON and TROBIT were combined with focussed data collection for this thesis. Plots from across the rainfall gradient, except for the dry forest limits, were chosen for resampling. These plots represented three forest types: wet evergreen, moist evergreen and moist semi-deciduous. To complete objective two, seven plots that had been previously burnt were compared to three unburnt plots in the same forest type. In total 31, 1 ha plots were included in analysis (Table 1.3).

Table 1.3. Plot Descriptions. Annual precipitation and consecutive dry months (< 100 mm precipitation) taken from WorldClim (Hijmans *et al.* 2005). All plots have one additional dry month in August. Use of each plot in the analyses of different chapters is indicated (x).

Forest Type	Forest Reserve	Plot Code	Latitude / Longitude	Plot Area (ha)	Census Years	Annual Precipitation (mm)	Consecutive Dry Months	Drought Chapter Composition Change	Drought Chapter Tree Height	Fire Chapter Fire Impacts	Fire Chapter Bark Thickness	Liana Chapter Temporal Change	Liana Chapter Spatial Patterns	Reference
Moist Semi-deciduous	Asenanyo	ASN-02	6.56 / -2.22	0.6	1993, 2007	1412	4	x	x			x	x	Lewis *et al.* 2009a
		ASN-04	6.48 / -2.17	0.88	1993, 2007	1432	4	x	x			x	x	
	Asukese	ASU-88	7.16 / -2.45	1	1990, 1995, 2010	1248	4		x	x	x			
		ASU-99	7.13 / -2.47	1	1989, 1995, 2006, 2010	1251	4		x	x	x			*TROBIT* & this study
		ASU-100	7.14 / -2.45	1	1989, 1995, 2006, 2010	1251	4		x	x	x			
		ASU-101	7.13 / -2.45	0.96	1989, 1995, 2006, 2010	1248	4		x	x	x			
	Bobiri	BBR-02	6.68 / -1.34	1	1990, 2010	1515	3		x	x	x			
		BBR-03	6.68 / -1.33	1	1990, 2010	1515	3		x	x	x			
		BBR-14	6.71 / -1.29	0.88	1990, 2010	1480	4	x	x	x	x	x	x	This study
		BBR-16	6.70 / -1.29	0.92	1990, 2010	1488	4	x	x	x	x	x	x	
		BBR-17	6.69 / -1.28	0.96	1990, 2010	1493	4	x	x	x	x	x	x	
		BBR-21	6.67 / -1.28	0.88	1990, 2010	1528	3		x	x	x			
	Esuboni	ESU-18	5.86 / -0.80	0.52	1993, 2010	1632	3	x	x		x	x	x	This study
		ESU-20	5.83 / -0.78	0.64	1993, 2010	1592	3		x		x			
	Kade	KAD-01	6.15 / -0.92	1	9 years 1968 - 2010	1641	3	x	x				x	Swaine *et al.* 1987 &
		KAD-02	6.15 / -0.92	1	8 years 1970 - 2010	1641	3	x	x				x	Lewis *et al.* 2009a
	Tinte Bepo	TBE-05	7.01 / -2.05	0.64	1990, 2010	1288	4		x		x			
		TBE-08	7.02 / -2.07	0.88	1990, 2010	1279	4	x	x		x	x		This study
		TBE-09	7.02 / -2.06	0.36	1990, 2010	1279	4		x		x			

Continued on next page.

	Forest Reserve	Plot Code	Latitude / Longitude	Plot Area (ha)	Census Years	Annual Precipitation (mm)	Consecutive Dry Months	Drought Chapter		Fire Chapter		Liana Chapter		Reference
								Composition Change	Tree Height	Fire Impacts	Bark Thickness	Temporal Change	Spatial Patterns	
Moist Evergreen	Bonsa River	BOR-05	5.35 / -1.83	1	1993, 2009	1659	3	x				x	x	This study
		BOR-06	5.35 / -1.84	1	1993, 2009	1660	3	x				x	x	
	Dadieso	DAD-03	5.97 / -3.03	1	1993, 2007	1658	3	x				x		Lewis *et al.* 2009a
		DAD-04	5.99 / -3.03	1	1993, 2007	1650	3	x				x		
	Tonton	TON-01	6.07 / -2.12	1	1991, 2010	1461	4	x				x	x	This study
		TON-08	6.04 / -2.10	1	1991, 2010	1457	3	x				x	x	
Wet Evergreen	Cape Three Points	CAP-09	4.85 / -2.10	1	1993, 2007	1733	3	x	x			x	x	Lewis *et al.* 2009a
		CAP-10	4.80 / -2.05	1	1993, 2007	1689	4	x	x			x	x	
	Draw River	DRA-04	5.16 / -2.38	1	1990, 2009	1921	3	x				x	x	This study
		DRA-05	5.21 / -2.44	1	1990, 2009	1928	3	x				x	x	
	Fure Headwaters	FUR-07	5.56 / -2.39	1	1990, 2009	1739	3	x				x	x	This study
		FUR-08	5.58 / -2.39	0.6	1990, 2009	1741	3	x				x	x	

2. Drought induced shifts in the floristic and functional composition of tropical forests in Ghana

2.1 Abstract

The future of tropical forests under global environmental change is uncertain, with biodiversity and carbon stocks at risk if precipitation regimes alter. This study assesses changes in plant functional composition and biomass in 19 plots from a variety of forest types over two decades of long-term drought in Ghana. The results show a consistent increase in dry forest, deciduous, canopy species with intermediate light demand and a concomitant decrease in wet forest, evergreen, sub-canopy and shade-tolerant species. These changes in composition are accompanied by an increase in above-ground biomass. The results suggest that by altering composition in favour of drought-tolerant species, the biomass stocks of these forests may be more resilient to longer-term drought than suggested by short-term studies of strong drought events.

2.2 Introduction

The risk of longer or more intense drought is one of the most pervasive threats faced by tropical forests (Laurance & Peres 2006; Lewis 2006). Though future climate projections are uncertain, particularly with regard to West Africa (Christensen *et al.* 2007), many IPCC-AR4 models predict reduced precipitation and long-term soil moisture droughts in some tropical and sub-tropical areas (Sheffield & Wood 2008). Many forests may therefore be exposed to increased drought intensity, frequency or longevity. However, few studies have assessed the response of tropical forests to longer-term drought. This study assesses the effect of a decadal-scale drought on the composition and structure of Ghanaian forests.

The effects of long-term reductions in rainfall are more complex than the impact of short-term droughts, as patterns of mortality and recruitment may cause a shift in community composition over time. For example, studies of two large plots in Central America demonstrated that floristic composition altered to favour deciduous, compound-leaved, canopy species with high wood density over a time period which included an episode of low rainfall (Condit *et al.* 1996; Condit 1998; Enquist & Enquist 2011; Feeley *et al.* 2011). Key questions are whether such changes in composition are observed over larger spatial-scales, and how they relate to changes in overall ecosystem function: if community composition shifts in favour of drought-tolerant species, forest carbon stocks may be more resilient to long-term drought than suggested by short-term studies of single drought events (van der Molen *et al.* 2011).

Monitoring forests over long periods that include droughts may be the only practical way to address these questions. Widespread networks of small plots have been effective in demonstrating consistent changes to tropical forest dynamics and structure across multiple sites (e.g. Phillips *et al.* 2009a; Lewis *et al.* 2009a, b) and in combination with a natural drought could be used to examine how forest composition and structure change in response to a long-term reduction in rainfall.

The results of monitoring can, however, be difficult to interpret, as many factors may influence the dynamics of the system. In order to assess whether drought is the dominant process affecting the composition of tropical forests it is necessary to consider other drivers of change, such as anthropogenic disturbance or other factors that may influence forest structure and composition. This can be achieved by comparing changes in the functional composition of communities to the changes that would be expected given different drivers (e.g. Parmesan & Yohe 2003; Lewis *et al.* 2009b). For example, if disturbances occurred during the monitoring period, increased light penetration would lead to an increase in the occurrence of low wood density, pioneer species (e.g. Verburg & van Eijk-Bos 2003) and a decrease in the occurrence of shade-tolerant species (e.g. Kariuki *et al.* 2006). In contrast, if the forests under study were recovering from disturbances that occurred before monitoring began, high wood density, shade-tolerant trees would be expected to increase (e.g. Chave *et al.* 2008a). Observations from plot networks have shown that many old growth tropical forests have increased in biomass in recent decades (Baker *et al.* 2004a, Lewis *et al.* 2009a) with increased atmospheric CO_2, fallout of nutrients from biomass burning or Saharan dust, and changes in solar radiation all suggested as possible causes (Chave *et al.* 2008a; Lewis *et al.* 2009b). Such increased resource availability has been hypothesised to affect species composition by favouring faster growing, canopy species that can capitalise on such resource increases (Laurance *et al.* 2004). In contrast, multi-decadal drought is likely to result in an increase in deciduous species that are associated with drier forest types (Enquist & Enquist 2011; Feeley *et al.* 2011). Drought, current disturbance, past disturbance and increased resource availability are therefore predicted to have different effects on the functional composition of forests (Lewis *et al.* 2009b). By investigating changes in the functional composition of a network of forest plots undergoing drought this study aims to assess whether the reduction in rainfall is the major driver of change in this system.

Monitoring the long-term effects of drought requires a forest region that has experienced a decrease in precipitation, a long-term phytodemographic dataset, and extensive ecological knowledge of the species. Ghanaian forests have these characteristics. West Africa has experienced drought since the 1970s (Dai 2011), perhaps linked to increasing sea surface temperatures (Shanahan *et al.* 2009; Dai 2011). In the forest zone of Ghana there has been a step-change in mean annual precipitation: rainfall in Kumasi, located within the forest zone, shows a reduction of approximately 250 mm yr^{-1} for the period 1980 - 2000 compared with 1950 - 1970 (Owusu & Waylen 2009). Additionally, the forest reserves of Ghana contain 600 one ha permanent sample plots established in the early 1990s (Affum-Baffoe 1996). By continuing to sample a subset of these plots and using an extensive trait data for Ghanaian forest species (Hall & Swaine 1981; Hawthorne 1995), it is possible to assess two decades of species dynamics in a variety of forest types during an extended drought. The results show that drought, rather than disturbance or increased resource availability, is most consistent with recent changes in the floristic and functional composition of these forests, and that this trend has been associated with an increase in aboveground biomass during the study period.

2.3 Material and Methods

2.3.1 Study Sites

Data were collected from a network of 19 long-term permanent sample plots of 0.52 - 1 ha in size from ten forest reserves located within wet evergreen, moist evergreen and moist semi-deciduous forest types in Ghana (Table 1.3, Fig. 2.4b). Plots were established by the Forestry Commission of Ghana (FCG) during the 1990s in unlogged forests and were re-censused between 2007 and 2010 as part of the current study. Most plots remained undisturbed during the study period. However, in 8 plots some subplots (covering 0.04 - 0.48 ha per plot) had been affected by tree felling; these subplots were removed from the dataset. All plots were located at least 150 m from the nearest forest edge, with the majority ≥ 1 km within a reserve (Table 2.4); fragmentation effects on forest dynamics are greatest within 100 m of the forest edge (Laurance *et al.* 1998) and therefore should not influence the results. None of the plots included in the study were known to have been burnt and at each site this was confirmed by examination of tree bases for evidence of fire scars. Although the precise long-term disturbance history of these plots is unknown, they all occur in old growth forest reserves, the majority of which were designated before 1940 (with the exceptions of Cape Three Points and Dadieso, which were established in 1950 and 1977 respectively). Data from two plots separated on the basis of soil type in other recent studies (Lewis *et al.* 2009a) were combined to keep plot size as consistent as possible.

In order to examine compositional changes since the onset of the drought (c. 1970), data from two long running one ha permanent sample plots at the University of Ghana Kade Agricultural Research Station (Swaine *et al.* 1987) were used, where multiple censuses have been completed from 1968 - 2010. The Kade dataset was analysed separately for three reasons: firstly, to make use of the multiple censuses associated with these plots, secondly, because this dataset extends to the beginning of the drought period and thirdly, because the plots are located in a 12.4 km^2 fragment adjacent to a Forestry

Commission; the Kade plots have therefore been subject to higher anthropogenic disturbance than those in the plots in the main analysis.

2.3.2 Precipitation Trends

Using the WorldClim dataset, recent long-term annual precipitation for each plot ranges from 1288 to 1928 mm (Hijmans *et al.* 2005, Fig. 2.4b). Rainfall is highest along the south-west coast and decreases inland. The rainfall pattern is bimodal; the main dry season (months < 100 mm precipitation) begins in November or December and ends in February, with an additional dry month in all sites in August.

To evaluate the long-term change in precipitation since the early 20th century, the Climate Research Unit (CRU) 1901-2006 TS3.0 dataset (Mitchell & Jones 2005) was used. To assess the accuracy of this global dataset for Ghanaian forests, it was compared to monthly data from four weather stations within the forest zone: Axim (data available for years 1961 - 2007), Kumasi (1961 - 2007) and Sunyani (1970 - 2007) from the Ghana Meteorological Agency, and Kade (1980 - 2009) from the University of Ghana. Correlations of monthly precipitation between the weather stations and CRU datasets were high (Axim: $r = 0.802$, Kumasi: $r = 0.797$, Sunyani: $r = 0.771$, Kade: $r = 0.630$) but wet season precipitation was underestimated by CRU, especially for Axim which is located on the very wet southern coast. The CRU data were therefore used only to assess temporal trends, rather than spatial patterns, in rainfall.

In all 10 CRU grid cells containing the study sites, annual precipitation was significantly higher for years pre-1970 than post-1970 (Table 2.1), decreasing by 165 mm yr^{-1} when averaged across all 10 grid cells. This value is lower than the reduction of 250 mm yr^{-1} presented by Owusu & Waylen (2009); however, the calculations are not directly comparable as Owusu & Waylen (2009) calculated their value for a different time period (excluding data from 1970-1980) and for a single location (Kumasi). The annual rainfall anomaly (averaged across all grid cells containing study sites) from the 1901-2006 mean clearly shows reduced rainfall after 1970 (Fig. 2.1). This decrease occurs all year round, with a higher absolute reduction during the wet season, but a proportionally higher reduction during the main dry season (22.8 % reduction compared with average pre-1970 dry season precipitation, compared with a 10.2 % reduction during the wet season). All sites experienced similar proportional reductions in precipitation.

Table 2.1. Mean annual precipitation pre- and post-1970 from Climate Research Unit (CRU) 1901-2006 TS3.0 dataset (Mitchell & Jones 2005) dataset for grid cells containing forest plots.

Reserves	MAP 1901-1969 (mm)	MAP 1970-2006 (mm)	t*	p*
Asenanyo, Tonton	1491	1310	4.92	<0.0001
Asukese, Tinte Bepo	1342	1184	4.22	<0.0001
Bobiri	1424	1228	5.76	<0.0001
Bonsa River	1384	1261	2.80	0.0064
Cape Three Points	1534	1378	3.48	0.0008
Dadieso	1627	1429	4.91	<0.0001
Draw River	1570	1407	3.86	0.0002
Esuboni	1207	1080	3.91	0.0002
Fure Headwaters	1513	1357	4.10	<0.0001
Kade	1338	1148	6.23	<0.0001

* t-value and p-value for t-test comparing precipitation of each year 1901-1969 and each year 1970-2006 for the relevant CRU grid-square.

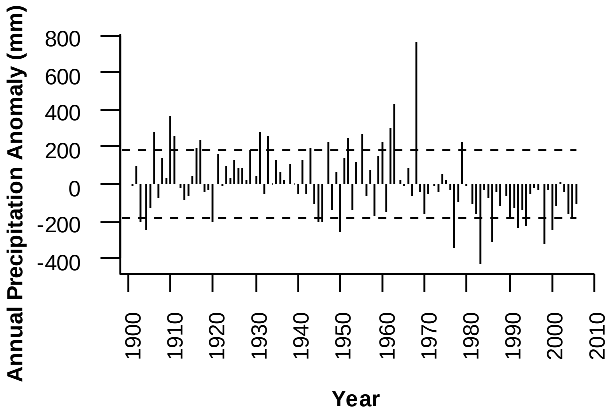

Figure 2.1. Annual precipitation anomaly (mm) from the 1901 - 2006 mean for the average annual rainfall across all grid squares containing plot locations (1901 - 2006 mean 1386 mm). Dashed lines represent 1 standard deviation from the mean. Data from CRU (Mitchell & Jones 2005).

2.3.3 Measurements

Initial plot set-up and measurements were performed following Alder & Synnott (1992) and re-measurements followed similar standard protocols (Phillips *et al.* 2009b). Each stem ≥ 10 cm *D* (diameter at breast height; 1.3 m or above buttresses) was given a metal reference tag, and *D* and species identity was recorded. Of 10,224 recorded stems, 97.3 % of trees were identified to species-level, 2.04 % to genus-level only, 0.03 % to family-level only, and 0.58 % were unidentified. Identification was carried out by employees of FCG for the initial census and by K.P. Duah and Y. Nkrumah (FCG), supplemented by J. Dabo of the Forestry Research Institute of Ghana (FORIG) and the use of the FORIG herbarium for the recent census.

2.3.4 Functional trait data set

Data was collated on species' habitat preferences, wood density, leaf phenology, adult canopy position and successional status. Habitat score was based on a detrended correspondence analysis (DCA, with rare species down-weighted) of an extensive independent dataset of presence of 1550 vascular plant species in 155, 0.0625 ha plots (Hall & Swaine 1976, 1981) and 552 inventory lists (Hawthorne & Abu Juam 1995) from across the forest zone of Ghana. The first axis of this ordination (eigenvalue = 0.36, gradient length = 4.38, total inertia = 6.68) shows a clear relationship with the wet to dry gradient across the forest zone (Fig. 2.2). Soil fertility covaries with rainfall due to a long history of leaching under higher precipitation regimes. However, overall the first axis scores are more strongly correlated with rainfall than soil fertility (see Swaine 1996 for further details). The value for each species along this axis was used as the habitat score for that species, with higher numbers referring to drier forest species. The full range of species scores from the original ordination was -259 to 687, and for species included in the plot network the range was -166 to 503. A habitat score was available for 97.1 % of species and 99.1 % of stems.

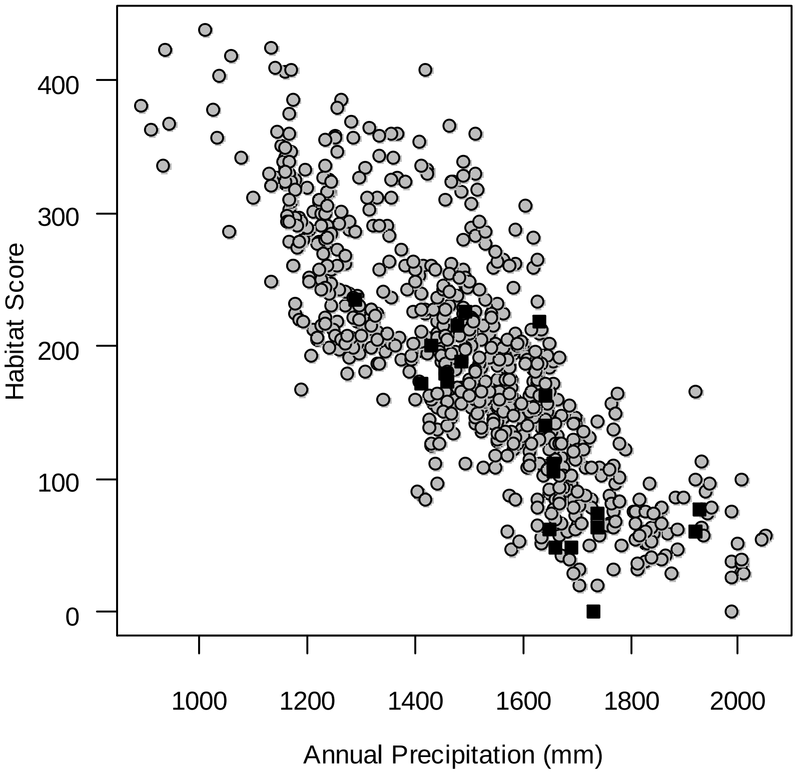

Figure 2.2. Relationship between habitat score and annual precipitation (mm) from WorldClim (Hijmans *et al.* 2005) for all data points used in the habitat score ordination (grey circles; data from Hall & Swaine 1976, 1981; Hawthorne & Abu Juam 1995) and plots included in the the analysis (black squares).

Wood density, ρ, was taken from the ForestPlots.net database (Zanne *et al.* 2009; López-González *et al.* 2011a; López-González *et al.* 2011b), assigned to stems at species level where possible, or given the genus or family-level mean as appropriate (Baker *et al.* 2004b, Flores & Coomes 2010). Species, genus, and family-level values were used for 65.4 %, 23.5 % and 8.3 % of stems respectively; in total 97.2 % of stems were allocated a wood density value. Data on leaf phenology, adult canopy position and successional guild were collated from Hawthorne (1995), Hall & Swaine (1981) and Poorter *et al.* (2004). Leaf phenology was classified as deciduous or evergreen (classification possible for 78.2 % of species and 91.8 % of stems). Where deciduousness was ambiguous (for instance where a species was stated as "sometimes deciduous") it was classified as deciduous (17 species). Adult tree canopy position was classified as understorey (< 10 m), sub-canopy (10-30 m) or canopy (> 30 m) (classification possible for 92.2 % of species and 97.8 % of stems). Successional guilds were defined as pioneer (unable to establish in closed forest shade), shade-tolerant (able to establish in closed forest shade) or non-pioneer light demander (NPLD - seedlings are present in the shaded understorey but require higher light environments to reach adult size) following Hawthorne (1995) (classification possible for 91.5 % of species and 97.4 % of stems).

2.3.5 Changes in biomass

To investigate changes in biomass stocks, annualised rates of biomass change were calculated using the moist forest allometric equation based on diameter and species wood density from Chave *et al.* (2005):

$$\text{Aboveground biomass} = \rho \times \exp(-1.499 + 2.148\ln(D) + 0.207(\ln(D))^2 - 0.0281(\ln(D))^3)$$

to calculate biomass at each census. Of the tropical biomass equations available, the Chave *et al.* (2005) moist forest equation was most suitable. This equation was chosen as the rainfall regimes of the study sites most closely match those defined as ‘moist’ by Chave *et al.* (2005) than those upon which the dry forest equation is based (sites in northern Australia, India and Mexico with long dry seasons of 5 to 8 months). In addition, a study of wet evergreen forests in Ghana showed that, of the available tropical biomass equations, the Chave *et al.* (2005) moist forest equation predicted biomass most accurately in this forest type (Henry *et al.* 2010). The dataset also includes samples from moist evergreen and moist semi-deciduous forest types that may show different allometric relationships.

As dry forests may contain shorter statured species with a lower height for a given diameter, height-diameter relationships for wetter and drier forest adapted species were assessed to ensure using a single biomass equation for all forest types and over time would not bias results. Height-diameter allometry was calculated based on a dataset of tree diameter at 1.3 m or above buttresses (D) and tree height (H) for 867 individuals from 21 plots (Table 1.3) located predominantly in the moist-semideciduous forest type, with two located in the wet evergreen forest type. Within each plot up to 50 trees were randomly selected to cover a wide range of diameter sizes and tree heights were measured using either a Haglöf Vertex III ultrasonic hyposometer, a Nikon Laser 550AS laser rangefinder, or by climbing the tree with a tape measure. Following Feldpausch *et al.* (2011) any trees known to have been broken or exhibiting crown damage were excluded from analysis. Using the habitat score for each individual (based on their species identification), the data were split into 'dry' (habitat score > 175; 604 stems) and 'wet' (habitat score < 175; 263 stems) forest species. The habitat score cut off was chosen based on the observation from the 2010 census data that plots located in wet or moist evergreen forest types typically had a stem-based plot-mean habitat score below 175, whereas plots located in moist semi-deciduous forests typically had a stem-based plot-mean habitat score above 175. Height-diameter curves based on power law relationships (e.g. Feldpausch *et al.* 2011) were produced for the dataset using nonlinear regression (Xiao *et al.* 2011), with separate models produced for each species classification (wet or dry). The equation $H = aD^b + \varepsilon$ was modelled, where a and b are constants and ε is error. The separate models of the two species classifications were not significantly different (F = 0.72, df = 341, $P = 0.99$, ANOVA; Fig. 2.3, Table 2.3). This shows that, contrary to the hypothesis that dry forest species would have a lower diameter for a given height, there is no significant difference in allometry between the two species classifications. Interestingly, for larger diameters (> 50 cm) the 'dry' forest species are taller than the 'wet' forest species (Fig. 2.3); the increased tree height of species present in the moist semi-deciduous forests has been shown in previous studies (Hall & Swaine 1981; Poorter *et al.* 2008). As the shape of the height-diameter relationship for drier forest species was not significantly different from the relationship for wetter forest species, the Chave *et al.* (2005) moist, rather than dry, forest biomass equation was used for all species and forest types in this analysis.

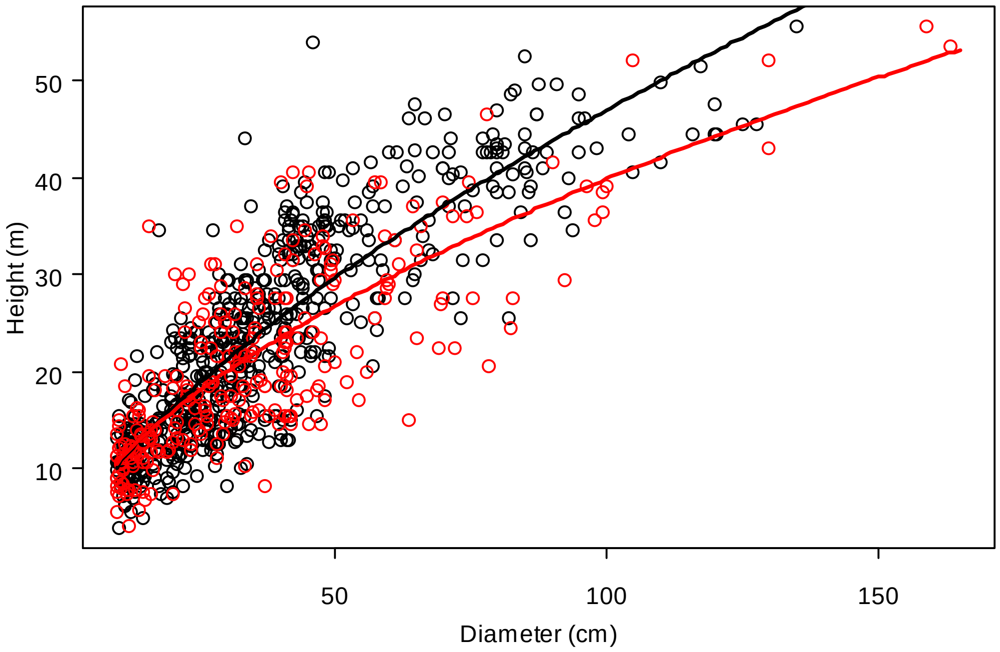

Figure. 2.3. Height-diameter curves for 'dry' (black) and 'wet' (red) forest species, separated on the basis of each species habitat score ('dry' species score > 175, 'wet' species score < 175). Each data point represents a single measured tree.

Table 2.2. Estimates of model parameters a and b for the equation $H = aD^b + \varepsilon$ for 'dry' and 'wet' forest species, estimated using non-linear regression. Species were separated on the basis of each species habitat score ('dry' species score > 175, 'wet' species score < 175).

Species Category	Parameter	Estimate	Standard Error	t-value	*p*
'Dry'	a	2.19	0.14	15.66	< 0.0001
	b	0.66	0.016	41.11	< 0.0001
'Wet'	a	2.78	0.29	9.63	< 0.0001
	b	0.58	0.027	21.79	< 0.0001

Where no species, genus or family-level wood density value was available for a stem, the plot-level mean was applied; missing species-level wood density values have been shown not to largely affect biomass estimates (Baker *et al.* 2004a, Flores & Coomes 2010). Where a change in the vertical point of measurement (POM) on the tree stem where the diameter was measured occurred, the *D* used in biomass estimation was the mean of *D* measurements at the original and new POM (2.5 % of stems). Where the original POM was not visible or thought to be incorrect, the first census *D* was back-calculated using the latest diameter measurement and the plot-level mean diameter growth rate (1.7 % of stems).

2.3.6 Plot-level trait shifts

To assess changes over time in the plot-level trait values, a similar bootstrapping method to that utilized by Feeley *et al.* (2011) was used. This method involved three steps: calculating plot-level trait values for each plot at each census, calculating the rate of change in each trait for each plot, and finally determining if the mean rate of change across all plots was significantly different from zero. First, for each continuous trait (habitat score, wood density) the plot-level trait score, x_j, for each census, j, was calculated as $x_j = \sum_{i=1}^{S} p_i \cdot q_i$ where S is the total number of species in the plot, p_i is the abundance of species i (based on stems or biomass) and q_i is the trait score of species i. For categorical variables (leaf phenology, adult canopy position and guild) x_j was simply calculated as the percentage of stems or biomass in each category. For example, for successional guild the percentage of pioneers were calculated, followed by the percentage of non-pioneer light demanders and then the percentage of shade-tolerant. Thus each category was treated separately. Species with a missing trait value were excluded from the analysis of that trait. Second, the annual rate of change of each trait was calculated as $(x_2-x_1)/t$, where x_1 is the initial plot-level trait score, x_2 is the final plot-level trait score and t is the census interval (years). Third, to test if the mean rate of change of a trait across the 19 sampled plots was significantly different from zero, 19 plots were randomly selected, with replacement, 5000 times, and calculated the mean rate of change of the trait, weighted linearly by plot size, for each bootstrap. If the 95 % confidence intervals (CI) from the distribution derived from the bootstrapped data (125th and 4875th ranked mean rate of change) did not overlap zero, it was considered that the change in that trait was significant (at the $p < 0.05$ level). For categorical variables, the method was performed twice, the second time using change in absolute numbers of stems or biomass in each category rather than change in percentage.

2.3.7 Species-level analysis

Species which significantly increased or decreased in abundance across the plot network were determined to assess whether species that showed similar changes in abundance also shared similar functional traits. A variation of the bootstrapping method of Laurance *et al.* (2004; 2006) that uses each plot as a replicate of the changes in species abundance was used. First, for each species the population size for the initial (N_1) and final (N_2) census was calculated, defined as the mean abundance of each species across all 19 plots at each census, based on stems or biomass, and weighted linearly by plot size. Second, the observed proportional change in population size (λ_o), as $\lambda_o = (N_2 - N_1)/N_1$, was calculated for each species. Third, a random selection of 19 plots were bootstrapped, with replacement, 5000 times. For each bootstrap N_1, N_2 and λ for each species was recalculated using the resampled selection of plots. The median value of λ across all species for each bootstrap, λ_m, was caluclated, 99 % CIs from the 5000 bootstraps were derived (25th and 4975th ranked values of λ_m). Species with λ_o above the upper 99 % CI or below the lower 99 % CI were deemed to have increased or decreased significantly more than the median species (at the $p < 0.01$ level). As only widespread species in occurring many plots can be analysed using this method, only species present in at least 6 of the 19 plots were included. This cut off excluded rare species whose population dynamics may show large stochastic fluctuations. This criterion gave a total number of 101 species from a total of 300 identified species. The median λ rather than the mean λ was used as some species showed large increases in abundance which subsequently inflated the mean, whereas the median is less sensitive to extreme values. 99 % CIs were used to assess significance to avoid spurious significant results from multiple tests of 101 species. The functional traits of species that had significantly increased and decreased were compared using t-tests and likelihood ratio (G) tests.

2.4 Results

2.4.1 Changes in forest structure

Above ground biomass of plots increased significantly during the census interval (mean interval 17.1 years; Fig. 2.4, Tables 2.3, 2.4) with a plot-size weighted mean increase of 1.78 Mg dry mass ha^{-1} yr^{-1} (bootstrapped 95 % CI = 1.09 – 2.48). Basal area also increased significantly during the census interval (Table 2.4) with a plot-size weighted mean increase of 0.12 m^2 ha^{-1} yr^{-1} (bootstrapped 95 % CI = 0.063 – 0.18). Changes in stem density differed markedly among plots and did not change significantly overall (plot-size weighted mean 0.032 stems ha^{-1} yr^{-1}, bootstrapped 95 % CI = -1.81 – 1.49, Table 2.4). The increase is biomass observed is therefore likely due to the increase in basal area.

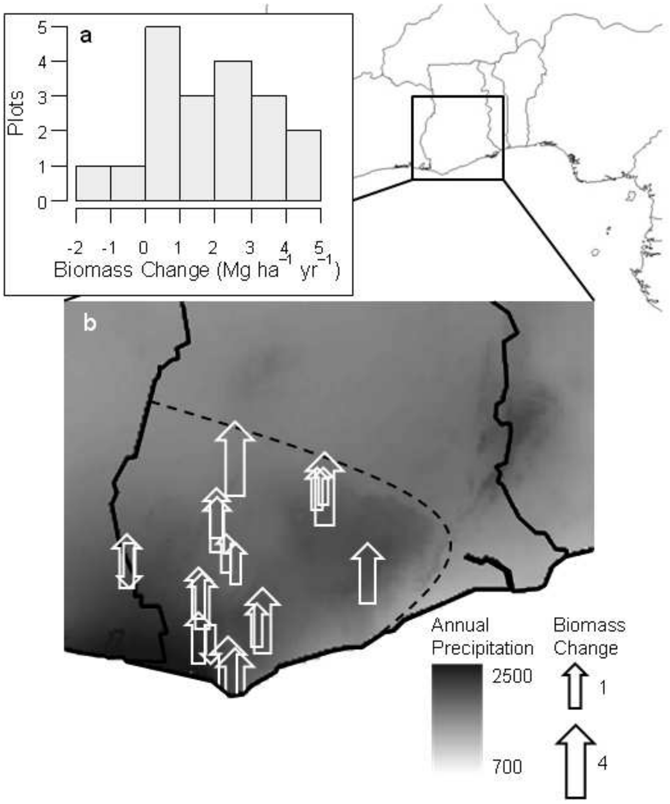

Figure 2.4. Location of plots and biomass changes. a) Histogram of annual rates of above ground biomass change (Mg ha^{-1} yr^{-1}). b) Mean annual precipitation (mm) of southern Ghana from WorldClim (Hijmans *et al.* 2005) with plot locations (approximate) and annual rates above ground biomass changes (arrows, size determines rate of biomass change, direction increasing or decreasing biomass, Mg ha^{-1} yr^{-1}), dashed line shows approximate edge of the forest zone.

Table 2.3. Plot structural variables for the initial and final censuses, for census dates see Table 1.3.

Forest Type	Plot Code	Distance to Edge (km)	Stem density (Stems ha^{-1})		Basal Area (m2 ha^{-1})		Biomass (Mg ha^{-1})		No. Species	
			Initial	Final	Initial	Final	Initial	Final	Initial	Final
Moist Semi-deciduous	ASN-02	1.27	632	612	31.1	32.9	318	339	82	87
	ASN-04	1.8	486	478	28.6	31.0	270	299	101	105
	BBR-14	0.15	495	508	27.6	27.8	304	321	87	84
	BBR-16	0.45	572	645	20.5	27.2	221	299	94	100
	BBR-17	2.3	458	501	30.7	31.2	345	351	78	73
	ESU-18	0.35	444	504	17.9	22.0	174	218	69	72
	KAD-01	0.78	557	480	27.8	23.9	332	280	84	89
	KAD-02	1.1	534	483	30.4	21.9	406	241	90	98
	TBE-05	1.0	500	497	20.9	26.4	221	302	74	71
Moist Evergreen	BOR-05	1.0	337	395	18.2	22.3	206	257	80	86
	BOR-06	2.0	430	486	20.4	22.0	241	256	87	91
	DAD-03	2.3	412	245	16.5	13.9	154	138	80	72
	DAD-04	2.9	456	445	25.7	27.0	356	385	93	91
	TON-01	1.15	458	394	28.7	28.1	378	385	62	63
	TON-08	2.2	483	464	28.6	29.5	315	327	88	92
Wet Evergreen	CAP-09	1.4	485	497	31.2	34.5	428	487	64	69
	CAP-10	1.1	427	449	20.1	23.1	194	248	97	97
	DRA-04	1.15	425	489	23.7	25.3	291	284	86	84
	DRA-05	1.0	422	447	24.3	27.1	273	306	82	83
	FUR-07	1.5	581	563	21.3	24.4	210	252	93	91
	FUR-08	1.15	582	520	20.4	22.2	204	235	72	80

* Annual Precipitation and consecutive dry months (< 100 mm precipitation) taken from WorldClim (Hijmans *et al.* 2005). All plots have one additional dry month in August.

† Dataset from the University of Ghana Agricultural Research Station at Kade, not part of the FCG plot network.

Table 2.4. Above ground biomass and stem density changes for each plot.

Plot	Rate of Biomass Change ($Mg\ ha^{-1}\ Yr^{-1}$)	Rate of Basal Area Change ($m^2\ ha^{-1}\ yr^{-1}$)	Rate of Stem Density Change ($stems\ ha^{-1}\ Yr^{-1}$)
ASN-02	1.53	0.126	-1.44
ASN-04	2.09	0.177	-0.57
BBR-14	0.89	0.0076	0.63
BBR-16	3.95	0.336	3.68
BBR-17	0.30	0.0288	2.10
BOR-05	3.14	0.254	3.60
BOR-06	0.94	0.102	3.52
CAP-09	4.24	0.231	0.86
CAP-10	3.89	0.216	1.57
DAD-03	-1.10	-0.181	-11.76
DAD-04	2.00	0.0915	-0.77
DRA-04	-0.35	0.0712	3.38
DRA-05	1.75	0.147	1.32
ESU-18	2.63	0.243	3.59
FUR-07	2.21	0.163	-0.96
FUR-08	1.61	0.0959	-3.25
TBE-05	4.07	0.274	-0.16
TON-01	0.42	-0.0328	-3.55
TON-08	0.72	0.0541	-1.07

2.4.2 Plot-level trait shifts

Community composition shifted in favour of drought-tolerant, deciduous, non-pioneer light demanding species. On a stems basis and using change in percentage for the categorical variables (Fig 2.5, Table A1), plot mean habitat score increased significantly (with higher scores reflecting drier species composition) during the study period (0.387 units yr^{-1}, 95 % CI = 0.203 – 0.565), as did the percentage of deciduous trees (0.108 pp yr^{-1}, 95 % CI = 0.031 – 0.197, pp is percentage point) and the percentage of non-pioneer light demanders (0.113 pp yr^{-1}, 95 % CI = 0.038 – 0.189). The percentage of shade-tolerant trees significantly decreased (-0.141 pp yr^{-1}, 95 % CI = -0.247 – -0.045). The percentage of canopy and sub-canopy trees did not change significantly. Based on absolute rates of stem change, deciduous trees significantly increased but changes in successional guild and canopy position were not significant (Table A1).

On a biomass basis and using change in percentage for the categorical variables (Table A2), patterns were similar to those based on stems. Significant increases were found for habitat score (0.429 units yr^{-1}, 95 % CI = 0.067 – 0.770), percentage of deciduous trees

(0.120 pp yr^{-1}, 95 % CI = 0.025 – 0.223), percentage of NPLDs (0.206 pp yr^{-1}, 95 % CI = 0.100 – 0.318) and percentage of canopy trees (0.190 pp yr^{-1}, 95 % CI = 0.095 – 0.290). Shade-tolerant (-0.138 pp yr^{-1}, 95 % CI = -0.262 – -0.022) and sub-canopy trees (-0.153 pp yr^{-1}, 95 % CI = -0.230 – -0.079) significantly decreased. Based on absolute biomass, increases in deciduous trees, NPLDs and canopy trees were significant but other changes were not.

In all stem and biomass analyses, changes in wood density, pioneer and understorey trees were not significant.

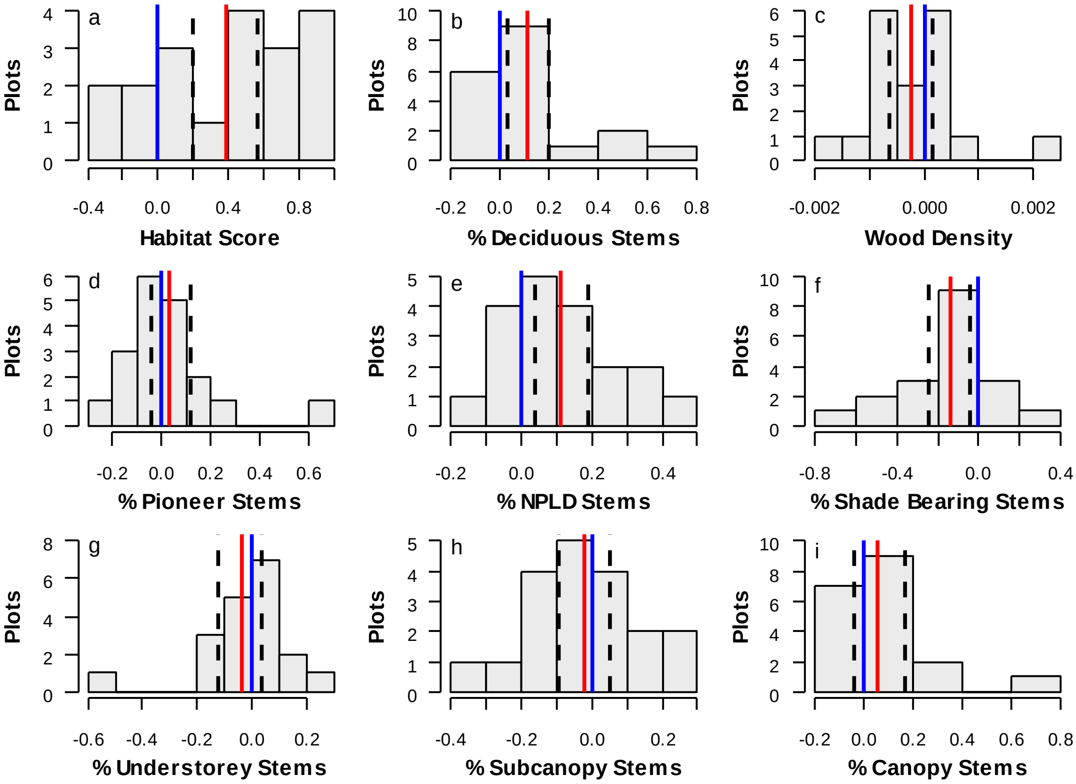

Figure 2.5. Histogram of annual rates of change in functional traits, based on stems. a) change in plot mean habitat score (where higher values relate to drier habitat species), b) change in % of deciduous stems, c) change in plot mean wood density (g cm^{-3}), d) change in % of pioneer stems, e) change in % of non-pioneer light demanding stems, f) change in % of shade bearing stems, g) change in % of understorey stems, h) change in % of subcanopy stems, i) change in % of canopy stems. Red lines - bootstrapped mean annual rate of change, dashed - 95 % confidence intervals and blue lines -zero change. Habitat score, deciduous, NPLD and shade-tolerant traits show significant directional change.

2.4.3 Change in species abundances

On a stem number basis, 32 species were found to be significantly increasing and 29 significantly decreasing (Table 2.5). On a biomass basis, 37 species were found to be significantly increasing and 39 species significantly decreasing (Table 2.5). Overall, 22 species increased and 22 decreased in both population change metrics, whilst four species increased in stem density but decreased in biomass and one species decreased in stem density but increased in biomass. The bootstrapped median population changes were 0.007 (99 % CI = -0.065 – 0.089) and 0.15 (99 % CI = 0.068 – 0.238) for stems and biomass respectively, where 0 indicates no change in population size. The median biomass-based population change was significantly greater than zero due to the increase in biomass across the plots (Fig. 2.6), whereas the median stem-based population change is close to zero as expected given the lack of overall change in stem density. The species showing the largest changes in abundance are typical of the plot-level functional shifts observed in the plot network, for example *Celtis zenkeri*, a deciduous, NPLD, canopy species showed a 107.5 % increase in biomass, whilst *Xylopia staudii*, an evergreen, shade tolerant, canopy species showed a 49.6 % reduction in stem number.

The percentage of deciduous species was significantly higher in the increasing compared to the decreasing species groups (45 % vs 22 %, and 40 % vs 25 % for stems and biomass, respectively; Fig 2.6; G-tests, stems: G = 6.17, df = 1, p = 0.013, biomass: G = 4.29, df = 1, p = 0.038). The percentages of understorey, sub-canopy and canopy species were also significantly different between increasing and decreasing species, with more canopy species and fewer sub-canopy and understorey species increasing in abundance (stems: G = 7.92, df = 2, p = 0.019, biomass: G = 14.88, df = 2, p = 0.0006). Increasing species groups had a lower percentage of shade tolerant and a higher percentage of NPLD species (stems: G = 8.65, df = 2, p = 0.013, biomass: G = 6.64, df = 2, p = 0.036) but pioneer species showed little difference between increasing and decreasing species groups. The mean habitat score of increasing species was higher than decreasing species, but this result was not significant. Mean wood density showed no significant difference between increasing and decreasing species groups.

Table 2.5. Increasing and decreasing species based on changes in stem density and biomass.

Increasing by stems	Decreasing by stems	Increasing by biomass	Decreasing by biomass
Allanblackia floribunda	*Aidia genipiflora*	*Anthonontha macrophylla*	*Aidia genipiflora*
Anthonontha macrophylla	*Albizia zygia*	*Antiaris toxicaria*	*Allanblackia floribunda*
Buchholzia coriacea	*Baphia pubescens*	*Buchholzia coriacea*	*Alstonia boonei*
Carapa procera	*Beilschmiedia mannii*	*Bussea occidentalis*	*Amphimas pterocarpoides*
Ceiba pentandra	*Bombax brevicuspe*	*Ceiba pentandra*	*Annickia polycarpa*
Celtis adolfi-friderici	*Calpocalyx brevibracteatus*	*Celtis adolfi-friderici*	*Baphia pubescens*
Celtis zenkeri	*Chrysophyllum subnudum*	*Celtis zenkeri*	*Beilschmiedia mannii*
Cola caricaifolia	*Cola nitida*	*Cola caricaifolia*	*Blighia unijugata*
Cola gigantea	*Discoglypremna caloneura*	*Cola gigantea*	*Bombax brevicuspe*
Cylicodiscus gabunensis	*Drypetes aylmeri*	*Daniellia ogea*	*Calpocalyx brevibracteatus*
Desplatsia chrysochlamys	*Drypetes principum*	*Desplatsia chrysochlamys*	*Cleistopholis patens*
Diospyros kamerunensis	*Hallea ledermannii*	*Dialium aubrevillei*	*Cola nitida*
Entandrophragma angolense	*Hexalobus crispiflorus*	*Diospyros kamerunensis*	*Corynanthe pachyceras*
Eribroma oblongum	*Klainedoxa gabonensis*	*Diospyros viridicans*	*Dacryodes klaineana*
Funtumia elastica	*Myrianthus libericus*	*Entandropragma cylindricum*	*Discoglypremna caloneura*
Guarea cedrata	*Newbouldia laevis*	*Funtumia elastica*	*Distemonanthus benthamianus*
Hannoa klaineana	*Panda oleosa*	*Guarea cedrata*	*Drypetes aylmeri*
Lannea welwitschii	*Pentadesma butyracea*	*Hannoa klaineana*	*Drypetes principum*
Memecylon lateriflorum	*Piptadeniastrum africanum*	*Irvingia gabonensis*	*Hallea ledermannii*
Musanga cecropioides	*Rinorea oblongifolia*	*Lannea welwitschii*	*Hexalobus crispiflorus*
Nesogordonia papaverifera	*Sterculia tragantha*	*Mammea africana*	*Microdesmis puberula*
Parkia bicolor	*Strombosia pustulata*	*Memecylon lateriflorum*	*Myrianthus libericus*
Petersianthus macrocarpus	*Tabernaemontana africana*	*Monodora myristica*	*Newbouldia laevis*
Polyalthia oliveri	*Treculia africana*	*Monodora tenuifolia*	*Petersianthus macrocarpus*
Pterygota macrocarpa	*Tricalysia discolour*	*Nesogordonia papaverifera*	*Pouteria altissima*
Pycnanthua angolensis	*Triplochiton scleroxylon*	*Parinari excelsa*	*Rinorea oblongifolia*
Ricinodendron heudelotii	*Vitex ferruginea*	*Piptadeniastrum africanum*	*Scottellia klaineana*
Sterculia rhinopetala	*Xylopia staudtii*	*Polyalthia oliveri*	*Scytopetalum tieghemii*
Trichilia monadelpha	*Xylopia villosa*	*Pterygota macrocarpa*	*Sterculia tragantha*
Trichilia prieureana		*Pycnanthua angolensis*	*Strombosia pustulata*
Uapaca guineensis		*Ricinodendron heudelotii*	*Tabernaemontana africana*
Zanthoxylum leprieurii		*Sterculia rhinopetala*	*Treculia africana*
		Trichilia prieureana	*Tricalysia discolour*
		Trilepisium madagascariense	*Trichilia monadelpha*
		Uapaca guineensis	*Trichillia tessmannii*
		Xylopia quintasii	*Triplochiton scleroxylon*
		Zanthoxylum gilletii	*Vitex ferruginea*
			Xylopia staudtii

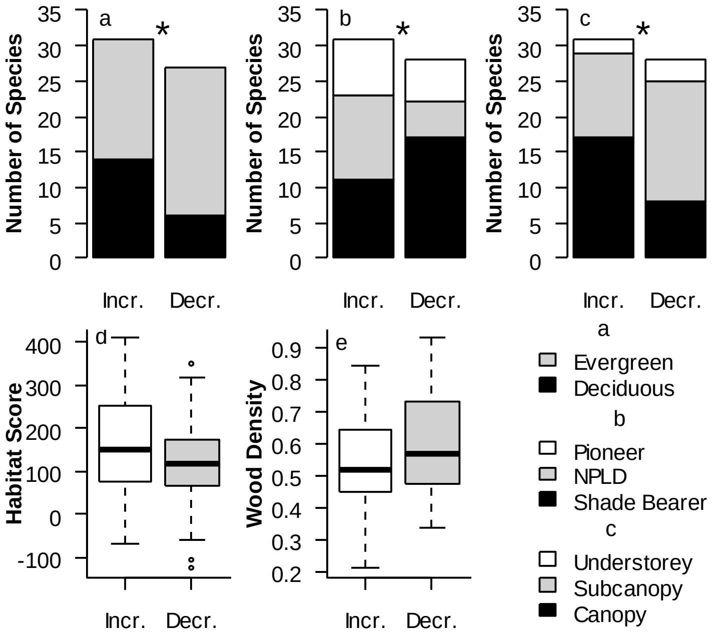

Figure 2.6. Characteristics of species significantly increasing and decreasing in stem population density. a) numbers of species classified as evergreen and deciduous in the increasing and decreasing species groups, b) numbers of species in each successional guild in the increasing and decreasing groups, c) number of species in each adult canopy position in the increasing and decreasing groups, d) boxplot of habitat scores and e) wood density (g cm^{-3}) of increasing and decreasing groups. * denotes a significant difference between increasing and decreasing species groups.

2.4.4 Trait shifts at Kade

The dataset spanning 1968 to 2010 of two, one ha plots showed very similar shifts in species composition to the plot network (Fig. 2.7). Most functional traits showed significant changes over time. Habitat score, percentage of deciduous, NPLD (KAD-01 only) and canopy trees increased, whilst the percentage of shade-tolerant and sub-canopy trees decreased ($p < 0.003$, $r^2 = 0.606 - 0.979$, Fig. 2.7). However, in contrast to the plot network, understorey trees significantly increased over time in KAD-01 (but not KAD-02). Pioneer trees and wood density, which showed no significant change in the plot network, significantly increased and decreased respectively in both Kade plots.

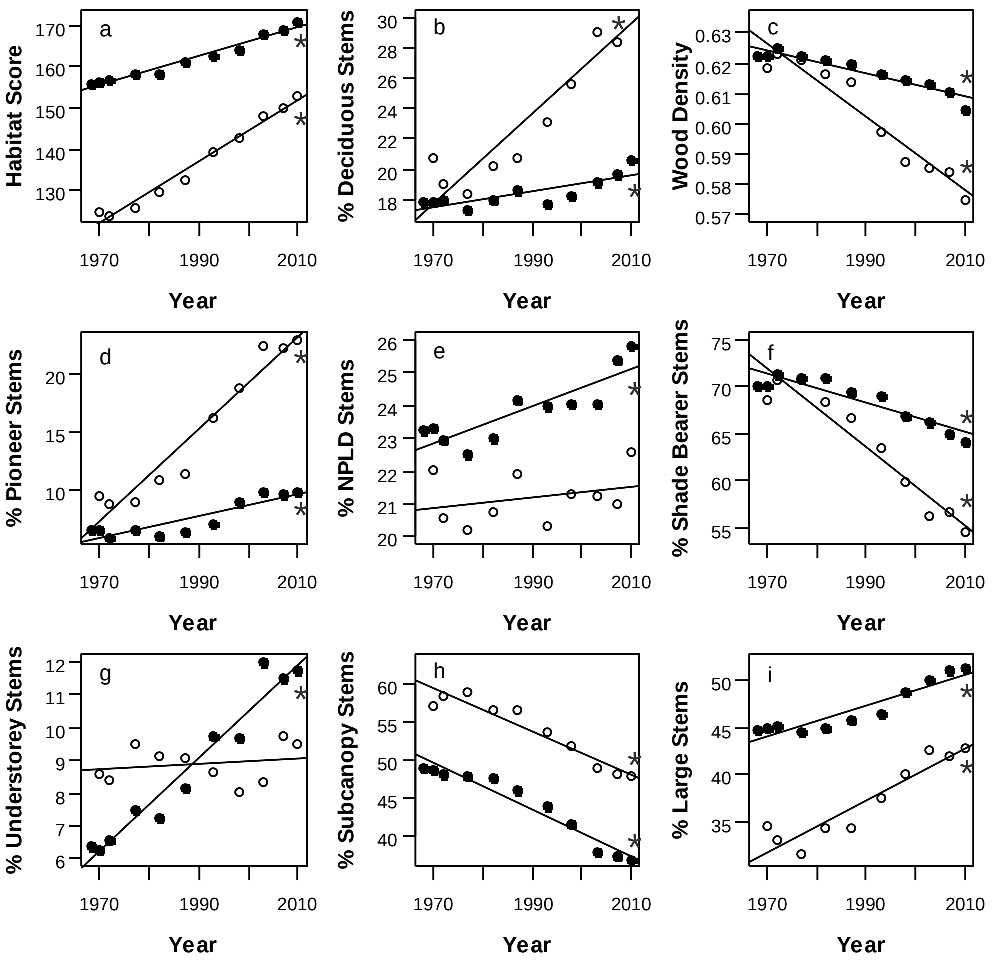

Figure 2.7. Changes in functional composition of KAD-01 (closed circles) and KAD-02 (open circles) from 1968 to 2010. a) change in plot mean habitat score, b) change in % of deciduous stems, c) change in plot mean wood density (g cm^{-3}) , d) change in % of pioneer stems, e) change in % of non-pioneer light demanding stems, f) change in % of shade bearing stems, g) change in % of understorey stems, h) change in % of sub-canopy stems, i) change in % of canopy stems. * denotes a significant change in trait over time.

2.4.5 Relationships between precipitation, traits and forest structure

Relationships between mean annual precipitation (WorldClim dataset, Hijmans *et al.* 2005) and both functional traits and forest structural variables are shown in Fig. 2.8. Relationships between continuous variables (habitat score, wood density, biomass, basal area and stem density) and precipitation were analysed using linear regression, and relationships between categorical variables (leaf phenology, guild and canopy position) and precipitation were analysed using Spearman's rank correlation. Many traits that showed significant trends across the plot network over time also show the equivalent significant relationships with MAP across the plot network (based on 2010 census data using number of stems, Fig. 2.8, Table 2.6, 2.7). In contrast, forest structural variables showed no significant relationships with MAP, despite biomass increasing over the census period (Fig. 2.8, Table 2.6, 2.7).

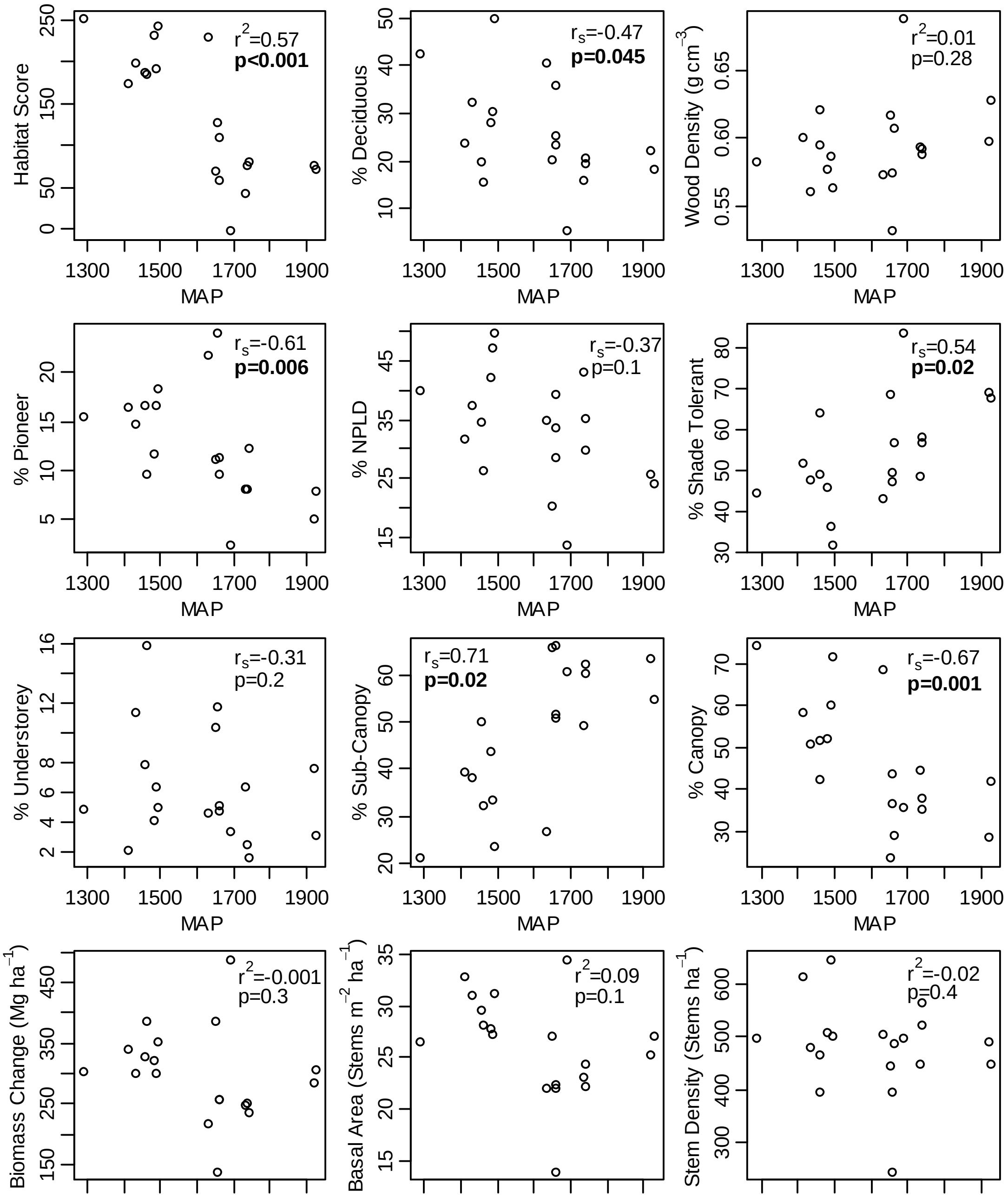

Figure 2.8. Relationships between mean annual precipitation (MAP (mm), data from WorldClim; Hijmans *et al.* 2005) and functional traits (top three rows) and forest structure (bottom row). Significant *p*-values from linear regression or Spearman's rank correlation are presented in bold.

Table 2.6. Results of linear regressions of precipitation as a predictor of continuous functional traits and forest structure variables. * denotes $p < 0.05$.

Variable	F	df	p	Adjusted r^2
Habitat Score	24.98	17	0.00011*	0.57
Wood Density (g cm^{-3})	1.24	17	0.28	0.013
Biomass (Mg ha^{-1})	0.98	17	0.34	-0.00097
Basal Area (m^2 ha^{-1})	2.74	17	0.12	0.088
Stem Density (stems ha^{-1})	0.71	17	0.41	-0.016

Table 2.7. Results of Spearman's correlations between precipitation and percentage of stems of different functional trait categories. * denotes $p < 0.05$.

Variable	S	p	r_s
% Deciduous	1674	0.045*	-0.47
% Pioneer	1840	0.0062*	-0.61
% NPLD	1564	0.12	-0.37
% Shade Tolerant	528	0.019*	0.54
% Understorey	1488	0.20	-0.31
% Sub-Canopy	336	0.0010*	0.71
% Canopy	1900	0.0024*	-0.67

2.5 Discussion

This is the first report from tropical forests of concerted species compositional shifts in response to drought across a range of sites and habitat types. Over the past two decades, species composition in Ghanaian forests has shifted to favour deciduous, drier-forest affiliated, canopy species with intermediate light requirements, over wetter-forest affiliated, evergreen, shade-tolerant, sub-canopy species. This suggests that changes to the rainfall regime are important in structuring these communities. In addition, the long term dataset at Kade provides evidence that these functional changes have been occurring since the onset of the West African drought.

2.5.1 Are widespread compositional changes likely to be caused by drought or other drivers?

The multiple drivers that may have led to the significant directional shifts in forest composition that were observed need to be carefully assessed. For example, disturbance during the study period was hypothesised to increase the abundance of pioneer and reduce the abundance of shade-tolerant species, while recovery from disturbance prior to monitoring would lead to an increase in shade-tolerant and a reduction in pioneer species (Chave *et al.* 2008a). However, although a reduction in shade-tolerant species was found, there was no change in the abundance of pioneer species, suggesting that neither current disturbance patterns nor recovery from past disturbance are the dominant drivers of compositional change in this dataset. A second potential explanation is related to increased resource availability, which has been hypothesised to favour fast growing, canopy species (Laurance *et al.* 2004). In this dataset, canopy species did increase in abundance but there was no trend in mean wood density, a proxy for diameter growth rate (King *et al.* 2006). These patterns are partially consistent with this hypothesis, as is the overall rise in aboveground biomass, suggesting that increased resource availability may be having a detectable effect on functional composition. Finally, drought was hypothesised to increase both deciduous species and species associated with drier forest types. Both of these patterns were found within the dataset (Fig. 3). Overall, considering the consistent trends in habitat score and deciduous species found across the plot network, drought, rather than disturbance or resource availability, appears to have been the dominant driver of compositional change. Furthermore, the case for drought as the driving force of changes in functional traits during the census period is supported by the finding that the traits that increased or decreased over time reflect the changes that occur spatially from wetter to drier forests (Fig. 8). For example, habitat score and the abundance of canopy trees increase in drier sites, whilst shade-tolerant and sub-canopy trees increase in wetter sites.

Despite these broad trends in compositional change across the plot network, some individual plots show patterns which reflect the importance of other drivers at smaller scales. For instance, DAD-03 exhibits a large increase in the percentage of pioneer trees (0.54 pp yr^{-1}) and reductions in biomass and stem density (Tables 2.4, A1-A2). These result from a strong disturbance during the census period. Surveying the site it was considered that the most likely cause of disturbance was an anomalous flooding event (S. L. Lewis, pers. obs.). The plot also shows large increases in drought-tolerant trees, with an increase in habitat score and one of the largest increases in the percentage of deciduous trees (0.54 % yr^{-1}). One explanation may be that the mortality event has allowed the changes seen in the other plots to be accelerated, as a greater proportion of trees in DAD-03 were replaced in the twenty year study period.

2.5.2 Longer-term change at Kade

The 40 year dataset from Kade shows very similar results to the plot network: habitat score, deciduous trees, NPLDs and canopy trees all increased, with a concurrent reduction in shade-tolerant and sub-canopy trees (Fig. 7). These changes occurred consistently over time, suggesting that the shifts seen since 1990 across the plot network have been ongoing since the onset of the West African drought and steadily continued throughout the census period to 2010. Pioneer species significantly increased and mean wood density significantly decreased over time suggesting that the Kade plots have experienced more disturbance than the majority of sites in the plot network. This trend is likely to be due to the small fragment size and possibly higher anthropogenic pressure on the Kade forest. In contrast to the plot network, understorey trees also increased over time in KAD-01. This is due to two tree species, *Diospyros canaliculata* and *Microdesmis puberula*, increasing in abundance. Other understory species remained rare or decreased throughout the study period. These two species have relatively high habitat scores, above the 70th percentile of all shade-tolerant species present in the plot. It is possible that the high drought-tolerance of these particular species may be allowing them to increase in abundance at this site.

2.5.3 Effects of long-term and short-term drought

The results presented here and from other long-term drought studies differ from those focusing solely on short-term, extreme droughts. Many studies of the impact of short-term droughts on mortality, typically linked to El Niño Southern Oscillation (ENSO) events, find that large trees suffer greater mortality than small understorey trees (Condit *et al.* 1995; Slik 2004; van Nieuwstadt & Sheil 2005; Phillips *et al.* 2010; but see Nakagawa *et al.* 2000). In addition, results from throughfall exclusion (TFE) experiments have also reported increased mortality of large trees (Nepstad *et al.* 2007; da Costa *et al.* 2010). In contrast, this study and those from Panama (Condit *et al.* 1996; Feeley *et al.* 2011) and Costa Rica (Enquist & Enquist 2011) show an increase in abundance of canopy trees and often a decrease in small trees. One explanation for this may lie in the types of drought that these studies cover. In TFE experiments 50 % of rainfall may be excluded (Nepstad *et al.* 2007; da Costa *et al.* 2010) and ENSO events characteristically reduce pan-tropical rainfall by approximately 30 % (Malhi & Wright 2004 p321) and often with much greater reductions at individual sites. Long-term droughts, however, can be more complex, with long-term reductions in precipitation which may or may not also be punctuated by stronger drought events. For example, the average decrease in annual rainfall in this study is 11 %, with some years experiencing especially low rainfall (Fig. 1). Precipitation at the site studied by Enquist & Enquist (2011) gradually decreased over the 20th century and included nine years of extremely low rainfall during the census period. At the study site in Panama annual precipitation declined by 11 % from 1965 to 1996 compared to pre-1965 precipitation (Condit *et al.* 1996), with a particularly strong drought during the 1982/83 ENSO event which the forest may still be responding to (Feeley *et al.* 2011). Although there is likely to be variability in drought strength over extended time periods, the rainfall declines in the long-term datasets are generally weaker than those of short-term studies or experimental droughts. Increased mortality of large trees may occur when soil water levels fall below a critical threshold (Nepstad *et al.* 2007) due to the high transpiration demand of canopy trees and the distance over which water must be transported (da Costa *et al.* 2010), resulting in hydraulic failure (Phillips *et al.* 2010). Smaller trees might be susceptible to drought-induced mortality at less severe reductions in soil water than canopy trees, possibly due to the higher likelihood of carbon starvation in a low light environment, or their shorter rooting depths (Condit *et al.* 1996). Longer-term but less extreme droughts may result in weaker soil water deficits, sufficient to impact small trees but not reaching the threshold at which canopy trees face physiological difficulties. Consistent with this, Phillips *et al.* (2010) found that the relative risk of mortality for large trees was lower where droughts were less severe.

Recent evidence shows that intact tropical forests have increased in biomass over decadal timescales (Baker *et al.* 2004a, Lewis *et al.* 2009a) and a variety of potential drivers have been proposed; increased resource availability from atmospheric CO_2, nutrient enrichment and solar radiation (Lewis *et al.* 2009b). In contrast, studies of anomalous short droughts and TFE studies have found rapid biomass loss over short periods (van Nieuwstadt & Sheil 2005; Phillips *et al.* 2009a; da Costa *et al.* 2010) showing that these extreme droughts can temporarily reverse the processes leading to increased biomass. Despite the long-term drought, this study found an increase in biomass of a similar magnitude to other African (Lewis *et al.* 2009a) and Amazonian (Phillips *et al.* 2009a) forests over recent decades. It is hypothesised that the shift in composition in favour of drought-tolerant species that was detected may play a key role in allowing the carbon stocks of these forests to be maintained during this long-term, low-intensity drought. As the forest structure is maintained, the driver(s) of widespread biomass increase may still be able to act on the system, whereas only during extreme droughts do increases in tree mortality dominate and cause substantial decreases in aboveground biomass.

The results presented here show species compositional change in response to drought in conjunction with an increase in biomass. However, scaling-up these results requires extreme caution. This study only assessed old growth sites and avoided areas with direct anthropogenic impacts or that had been subject to wildfires; thus, these sites are not representative of Ghanaian forests which are typically subject to high levels of human activity and in which disturbance, or in some areas fire, are likely to play an important role. Furthermore, extrapolating results to other parts of the tropics should be done with care. The West African species pool may contain a particularly large proportion of disturbance- and drought-adapted taxa compared to other tropical forests for three reasons. Firstly, West African forests may have experienced such droughts as part of an approximately 40 year wet – dry cycle operating over the past several thousand years (Shanahan *et al.* 2009). Secondly, forests generally occur in Africa under lower precipitation than in other tropical areas and have experienced dry periods during glacial-interglacial cycles (Anhuf *et al.* 2006). Thirdly, though forests globally have been subject to some level of human activity for thousands of years, humans have been present in Africa for a greater time than other areas of the tropics (Barnosky *et al.* 2004) and West African forests have been fragmented and exposed to high levels of recent anthropogenic disturbance (Fairhead & Leach 1998). Other tropical forest regions may not be so well-stocked with species adapted to such changes in the environment.

In conclusion, this study shows the importance of changes in species composition within a forest stand in determining the response of tropical forests to long-term drought. While highlighting the sensitivity of tropical forest composition to environmental change it is also demonstrated that the range of strategies represented within species-rich forests means that some drought events may not result in reductions in forest carbon stocks.

3. Long-term impacts of understorey fires on tropical forest structure and functional composition in Ghana, West Africa.

3.1 Abstract

Tropical forests are at increasing risk of fire due to the synergistic effects of anthropogenic disturbance and drought events. Despite this, the long-term impacts of fire on tropical forests and the post-fire trajectories of burnt areas are not well quantified. Previous studies up to 15 years after fires show evidence of regeneration of forest structure but little recovery of forest composition. In this study, post-fire regeneration is explored using a unique 27 year dataset of 10, one ha plots from Ghana. The forest structure in 2010 of plots previously burnt once (in 1983) or twice (in 1983 and 1995) was significantly related to previous fire intensity, with stem density reduced by up to 67 % compared with unburnt plots. The composition of the plots remained similar to disturbed areas and showed little sign of recovery. However, aboveground biomass and stem density had increased in burnt plots since the fires, suggesting that forest structure was recovering. The results confirm that understorey fires have a substantial impact on forest structure and composition and that forest structure recovers faster than forest composition. It is estimated that 15 - 70 years would be required for full regeneration of biomass stocks and stem density in burnt plots, with variation strongly linked to previous fire intensity.

3.2 Introduction

The frequency of fires in tropical moist forests has increased considerably in recent years (Peres *et al.* 2006). Current fire-return intervals (e.g. Eastern Amazon, 82 years, based on remotely sensed burn scars for a 23 year period; Alencar *et al.* 2011) are much shorter than the background rate (e.g. Venezuelan Amazon, 400 - 1560 years, based on charcoal records dated 250 - 6000 years BP; Sanford *et al.* 1985). These increases in fire occurrence are linked to human activities, such as selective logging (Holdsworth & Uhl 1997) and fragmentation (Cochrane 2001; Cochrane & Laurance 2002) which increase forest flammability by increasing fuel load and opening the forest canopy, in combination with agriculture and cattle ranching which provide ignition sources (Uhl & Buschbacher 1985). Forest flammability is increased further by extreme droughts, such as those associated with El Niño Southern Oscillation (ENSO) events in some regions, which dry out potential fuels on the forest floor. The combination of drought, fragmentation, logging and ignition sources has led to vast areas of forest burning (e.g. Brazilian Amazon, 3.9 million ha burnt during the 1998 ENSO; Alencar *et al.* 2006). Future trends in deforestation and climate change are likely to increase further the probability of fires in remaining tropical forest fragments; simulations of future Amazonian fire regimes suggests climate change, deforestation and road building could lead to a doubling of fire occurrence by 2050 (Silvestrini *et al.* 2011).

Fires are clearly a major threat that will affect the future structure and composition of tropical forests, but the impacts and particularly the ability of previously burnt forest to recover, are unclear. Research on the response of forests to fire has produced highly variable results and the majority of studies have focussed on relatively short-term post-fire periods. For example, a number of studies have reported enhanced mortality of trees, ranging from 8 to 90 % of stems dying due to fire events (Barlow & Peres 2006) and small trees with thin bark are particularly vulnerable to fire-induced mortality (Uhl & Kauffman 1990; Cochrane & Schulze 1999; Barlow *et al.* 2003a; van Nieuwstadt & Sheil 2005; Balch *et al.* 2011; Brando *et al.* 2012). The spatial variation in mortality can be attributed both to fires occurring in different forest types where the susceptibility of the tree community to fire varies, and also to differing fire intensities. For example, fire-associated mortality rates reported from core Amazonian forests are higher than those from the Amazon fringe which may contain fewer susceptible tree species due to prior exposure to fire from the forest-savannah transition zone (Barlow & Peres 2006). Within a single area of forest there can also be considerable variation in fire intensity, resulting in variation in the impacts of fire on the vegetation (Cochrane & Schulze 1999). In general, fire intensity, estimated using the presence and heights of fire scars on tree boles, is a strong predictor of changes in forest structure due to fire (Barlow *et al.* 2003; Barlow & Peres 2004; Balch *et al.* 2008; Brando *et al.* 2012). However, although these studies demonstrate substantial immediate impacts of fire, the long-term trajectories of previously burnt areas have been little studied.

The majority of studies measure the effects of fire within 3 years of the fire event (Cochrane & Schulze 1999; Barlow *et al.* 2003a; van Nieuwstadt & Sheil 2005) and such short post-fire periods do not allow insight into forest regeneration after burning and how long the effects persist. The current longest studies of recovery following fire suggest that that forest structure may regenerate but forest composition remains altered. For example, one of the longest post-fire studies measured five previously selectively logged 0.3 ha plots 15 years after a severe fire event in Borneo. Stem densities had recovered 5 - 15 years after fire, but species composition remained altered with a high density of pioneer species (Slik *et al.* 2002). Similar results were found in one 0.25 ha plot measured 18 years after fire in Nigeria (Muoghalu 2006), and four 0.25 ha plots measured 9 years after fire in the Brazilian Amazon (Barlow & Peres 2008). However, the small plot size, low numbers of replicates and relatively short time periods assessed by these studies are not sufficient to determine if the patterns found can be generalised, or whether the impacts of fires persist over longer timescales. Given the likely future increases in fire occurrence (Silvestrini *et al.* 2011) it is important to improve our understanding of these recovery processes following fire events.

Moist tropical forests in Ghana provide a unique opportunity to investigate the long-term patterns of recovery from ground fires. A strong ENSO drought affected much of the tropics during 1982/83 and led to fires in the 1983 dry season in Ghana (Swaine *et al.* 1992; 1997), as well as in other areas such as South-East Asia (e.g. Slik *et al.* 2002). Fires also occurred in some Ghanaian forest reserves during 1995 (Doe 2008). An extensive network of one ha permanent sample plots was established in Ghanaian forest reserves during the early 1990s, with some these plots located in burnt areas. By revisiting a sample of these plots in areas which experienced understorey fires and also in unburnt sites, this study assesses the extent to which forest structure and functional composition have recovered up to 27 years since the most recent fire. This dataset provides the longest directly observed record of tropical forest regeneration after understorey fires.

3.3 Methods

3.3.1 Study Sites

Data were collected from 10, 1 ha permanent sample plots from two forest reserves (Asukese: ASU and Bobiri: BBR) in the moist semi-deciduous forest zone of Ghana (Table 1.3, Table 3.1). Plots were established between 1989 and 1990 by the Forestry Commission of Ghana (FCG) and remeasured in 2010, resulting in a twenty year period of plot monitoring. Plots in ASU were also censused in 1995 and 2006 (except ASU-88 in 2006). In five of the plots, some sub-plots (covering 0.04 - 0.12 ha per plot) were affected by tree felling after establishment; these sub-plots were removed from analyses and plot sizes were reduced accordingly. The fire history of each plot was determined by assessing the bases of individual trees for fire scars (Barlow *et al.* 2010), from interviews with local residents, and consultation of FCG documents. Three plots in BBR remained unburnt throughout the study period, three plots in BBR were burnt in 1983 only (once burnt) and four plots in ASU were burnt in 1983 and 1995 (twice burnt, 1995 fire occured in January before the 1995 census).

Table 3.1. Details of census years and fire history of plots included in the study.

Reserve	Plot Code	Plot Area[a]	Census Years	Number of Fires[b]	Fire Intensity[c]
Bobiri	BBR-14	0.88	1990, 2010	0	0
	BBR-16	0.92	1990, 2010	0	0
	BBR-17	0.96	1990, 2010	0	0
	BBR-02	1	1990, 2010	1	0.41
	BBR-03	1	1990, 2010	1	0.27
	BBR-21	0.88	1990, 2010	1	0.21
Asukese	ASU-88	1	1990, 1995, 2010	2	1.2
	ASU-99	1	1989, 1995, 2006, 2010	2	0.66
	ASU-100	1	1989, 1995, 2006, 2010	2	0.51
	ASU-101	0.96	1989, 1995, 2006, 2010	2	0.29

[a] Plot areas were reduced in locations subject to tree felling.

[b] Fires occurred in 1983 once burnt forests and 1983 and 1995 in twice burnt forests.

[c] Fire intensity based on presence and heights of fire scars on tree boles (see Section 3.3.2).

3.3.2 Measurements

Initial plot set-up and measurements were performed following Alder & Synnott (1992). Re-measurements followed standard protocol (Phillips *et al.* 2009b). Each tree stem ≥ 10 cm *D* (diameter at breast height; 1.3 m or above buttresses) was given a metal reference tag and *D* and species identity recorded. Of 5001 stems, 99.4 % trees were identified to species-level, 0.36 % to genus, 0.04 % to family; 0.22 % remained unidentified. Identification was carried out by employees of FCG for the initial census and by K.P. Duah and Y. Nkrumah (FCG), supplemented by J. Dabo of the Forestry Research Institute of Ghana (FORIG) and the use of the FORIG herbarium for the recent census.

As fire intensity can be spatially variable within a single forest area (Cochrane & Schulze 1999) the presence and estimated heights of fire scars were recorded (Barlow *et al.* 2010) on every tree during the 2010 census as a proxy for fire intensity. Fire scar height is highly correlated to fire line intensity (Van Wagner 1973) and has been used to estimate fire intensity in other studies (Barlow *et al.* 2003a; Barlow & Peres 2004; Balch *et al.* 2011; Brando *et al.* 2012). Following Barlow *et al.* (2003a) each tree was categorized as 0 - no fire scar, 1 - scar up to 30 cm, 2 - scar 30 cm to 1.3 m or 3 - scar height above 1.3 m. A fire intensity score for each burnt plot was calculated as the mean scar category score (Barlow *et al.* 2003a; Barlow & Peres 2004). Only stems that had survived since the initial census were used to calculate the fire intensity measure in order to avoid including stems recruited since the fire that could not have been burnt. For twice burnt plots this measure is a composite of fire scars produced by the 1983 and 1995 fires. This measure of fire intensity is comparable between plots but may underestimate intensity when compared with other studies using the same method with measurements taken shortly after fires, as after 15 - 27 years many burnt trees may have died by the time the scars were recorded.

3.3.3 Functional Traits

To assess fire related changes to the functional assemblage of stands, data on species functional traits were collated from Hawthorne (1995), Hall & Swaine (1981) and Poorter *et al.* (2004). For each species a successional guild was applied, either pioneer, non-pioneer light demander or shade-tolerant (classification possible for 94 % of species and 99 % of stems). Adult canopy position was assigned as either understorey (> 10 m), sub-canopy (10-30 m) or canopy (>30 m) (classification possible for 91 % of species and 98 % of stems). Leaf phenology was categorised as deciduous or evergreen (classification possible for 81 % of species and 95 % of stems). Wood density was taken from values contained within the ForestPlots.net database (Zanne *et al.* 2009; López-González *et al.* 2011a; López-González *et al.* 2011b), and assigned to stems at a species-specific level where possible, or given the genus or family-level mean as appropriate (Baker *et al.* 2004a). Species-level values were available for 71 % of stems, genus-level values were used for 20 % of stems and family-level for 8 % of stems; in total 99 % of stems were allocated a wood density value.

As bark thickness has been proposed as a species trait determining fire tolerance (Uhl & Kauffman 1990, Barlow *et al.* 2003a, van Nieuwstadt & Sheil 2005), the bark thickness of all trees in both burnt and unburnt plots was measured using a Haglof bark gauge during the 2010 census in order to produce a species-specific bark thickness index. Four bark thickness measurements were taken around the trunk of each tree at approximately 1.1 m from the ground. Individual tree bark thickness was calculated as the average of the four measurements. Bark thickness data was available from all ten plots included in this study as well as five additional plots within the moist semi-deciduous forest zone; all were included in this analysis. As bark thickness increases with D and varies between species (Paine *et al.* 2010), different models of bark thickness with dbh were tested to find the best model to fit the data. Only species with ≥ 3 sampled individuals were included in the analysis, resulting in a dataset of 164 species (all species combined n = 6569). Using the best model, the bark thickness of a 20 cm D stem was calculated for each species and this value was used as a species-specific index of bark thickness.

3.3.4 Biomass Calculations

Biomass stocks were calculated using the moist forest allometric equation based on diameter and species wood density from Chave *et al.* (2005). Where no species, genus or family-level wood density value was available for a stem, the plot level mean was applied. Where changes in the point of measurement (POM) occurred between censuses, the D used in biomass estimation was the mean of D measurements at the original and new POM (6.4 % of stems). Where the original POM was not visible or thought to be incorrect, the first census D was back-calculated using the latest diameter measurement and the mean diameter growth rate of the relevant plot and size class (0.6 % of stems).

3.3.5 Data Analysis

As no pre-fire data were available for the burnt plots, it was assumed that their structure and functional composition was comparable to the unburnt ~~control~~ plots. Such assumptions have been made in other similar studies (e.g. Cochrane & Schulze 1999; Slik *et al.* 2002; Barlow & Peres 2004; Barlow & Peres 2008). Unburnt plots were located in the same forest reserve (Bobiri) as the once burnt plots, which was 140 km from the reserve containing the twice burnt plots (Asukese). Both reserves were in the moist-semideciduous forest type, receive similar mean annual rainfall (1500 and 1250 in Bobiri and Asukese respectively), experience similar seasonality (3-4 consecutive dry months, > 100 mm) and have similar soil physical and chemical characteristics. As the twice burnt plots were located in a different reserve to unburnt plots, the unburnt plots cannot be considered as true controls, but are used a general comparison of forest structure, dynamics and functional composition in an area unaffected by fire.

3.3.6 Fire impacts on structure and dynamics after 27 years

To assess the impacts of past fires on current plot-level forest structure, linear regressions were used to relate structural variables to past fire intensity score. The structural variables were stem density (stems ha^{-1}), aboveground biomass (Mg ha^{-1}) and proportion of small trees ($D < 30$ cm). The relationships between post-fire forest dynamics and past fire intensity score were also assessed using linear regression. The dynamics variables were stem mortality for all trees and mortality of small ($D < 30$ cm) and large ($D \geq 30$ cm) trees, stem recruitment rate, biomass mortality, biomass recruitment and biomass growth rates (referring to the plot-level biomass increase due to growth of surviving stems). These rates were calculated using the equations presented in Lewis *et al.* (2004) and based on data for the entire census period (1990 - 2010) for the control and once burnt plots. For the twice burnt plots, the period 1995 - 2010 was used for these calculations to exclude the immediate mortality effects of the second fire on forest dynamics, as regeneration was the focus of the study.

3.3.7 Fire impacts on functional composition

The impact of past fire intensity on current plot-level functional traits was also determined using linear regression. The plot-level mean (for continuous variables; bark thickness and wood density) or percentage in each category (for categorical variables; guild, leaf phenology and adult canopy position) for each trait based on number of stems were calculated for the 2010 censuses. Stems without trait data were excluded from the analysis of that trait. The plot-level trait means or percentages were then regressed against past fire intensity score.

To determine the causes patterns between trait composition and fire intensity, be it trait-specific mortality at the time of the fire, mortality during the subsequent census period, or recruitment during the subsequent census period, patterns of recruitment and mortality in the post-fire period were assessed. Plot-level trait means and percentages based on the stems that died or recruited during the census interval were calculated. As for forest dynamics, the census intervals assessed were 1990 - 2010 for control and once burnt plots and 1995 - 2010 for twice burnt plots. If relationships between the 2010 functional composition and past fire intensity score were driven only by initial fire-induced mortality, there would be no relationship between the functional composition of subsequent recruits or dead trees and past fire intensity score. If relationships between the 2010 functional composition and past fire intensity score were driven only by mortality occurring in the post-fire period a relationship between the functional composition of trees that subsequently died and past fire intensity score would be expected. If the 2010 functional composition was determined only by post-fire recruitment, there would be a relationship between the functional composition of recruited trees and past fire intensity score. All percentages were arcsine transformed prior to analysis.

3.3.8 Fire impacts on floristic composition

To assess the differences in plot floristic composition with fire intensity and over time non-metric multidimensional scaling (NMDS, using Hellinger distance (Legendre & Gallagher 2001) was used; function metaMDS in R package vegan, Oksanen *et al.* 2011). This ordination was based on the abundance of stems of each species in the plots. Permutation multivariate analysis of variance based on similarities (function adonis in R package vegan, Oksanen *et al.* 2011) was used to test the effects of fire intensity, time and plot on floristic similarity. Analyses were performed separately for each of the two forest reserves to limit the effect of between-reserve compositional differences on results.

3.3.9 Estimation of initial fire impacts on stems and biomass

Many studies on the impacts of fires report the percentage of stems or biomass lost due to the fire, and studies of carbon emissions from fires use such measures in their calculations (e.g. Alencar *et al.* 2006; Silvestrini *et al.* 2011). As no data was collected in 1983 before the first fires occurred, percentages of stems and biomass lost to these fires were estimated. Given the available data, this process was necessarily complex. The mean stem density and biomass values estimated for 1983 for the unburnt plots were used as a reference with which to compare the estimated 1983 stem density and biomass values of the burnt plots. Estimated (post-fire) 1983 stem and biomass values were back calculated from the initial 1990 census values. To do this, plot specific rates of recruitment, mortality and growth were calculated for the period 1990 - 2010, and applied to the initial 1990 census values assuming that the forest dynamic rates for the period 1983 - 1990 were the same as from 1990 - 2010. For the twice burnt plots, plot specific rates could not be used as the 1990 - 2010 rates could be influenced by the second fire in 1995. For these plots, the mean dynamic rates of the once burnt plots were applied to the initial census stem density and biomass values of the twice burnt plots to estimate the 1983 values. Finally, the percentage differences between the estimated burnt plot 1983 stem density and biomass values and the estimated unburnt 1983 reference values were then calculated. The results associated with this method are uncertain, due to the number of assumptions made in their calculation. This uncertainty derives from three sources. First, the assumption that biomass and stem densities of burnt plots were similar to the unburnt plots before the fires occurred; second, that the dynamic rates of recruitment, growth and mortality during the census period (1990 - 2010) were the same as for the initial post-fire period (1983 - 1990); and third that the dynamic rates of the twice burnt plots in the initial post-fire period were the same as those for the once burnt plots. All of these assumptions are likely to be incorrect to some extent, and therefore caution should be taken when considering the estimated percentage losses due to the 1983 fires. However, as many studies report or use these values, they have been included here.

3.4 Results

3.4.1 Species specific bark thickness

A log-log relationship between bark thickness and *D* best described the data (Fig. 3.1). Linear regression was used to model bark thickness (log transformed) as a function of *D* (log transformed) and species (Fig. 3.1). Both *D* and species were significant predictors of bark thickness (Table 3.2). Bark thickness at 20 cm *D* for each species ranged from 2.7 mm to 8.8 mm (classification possible for 72.5 % of species and 97.9 % of stems) which was within the range of observed bark thicknesses at that diameter size (2.3 - 10.0 mm for trees 19.7 cm > *D* < 20.3 cm).

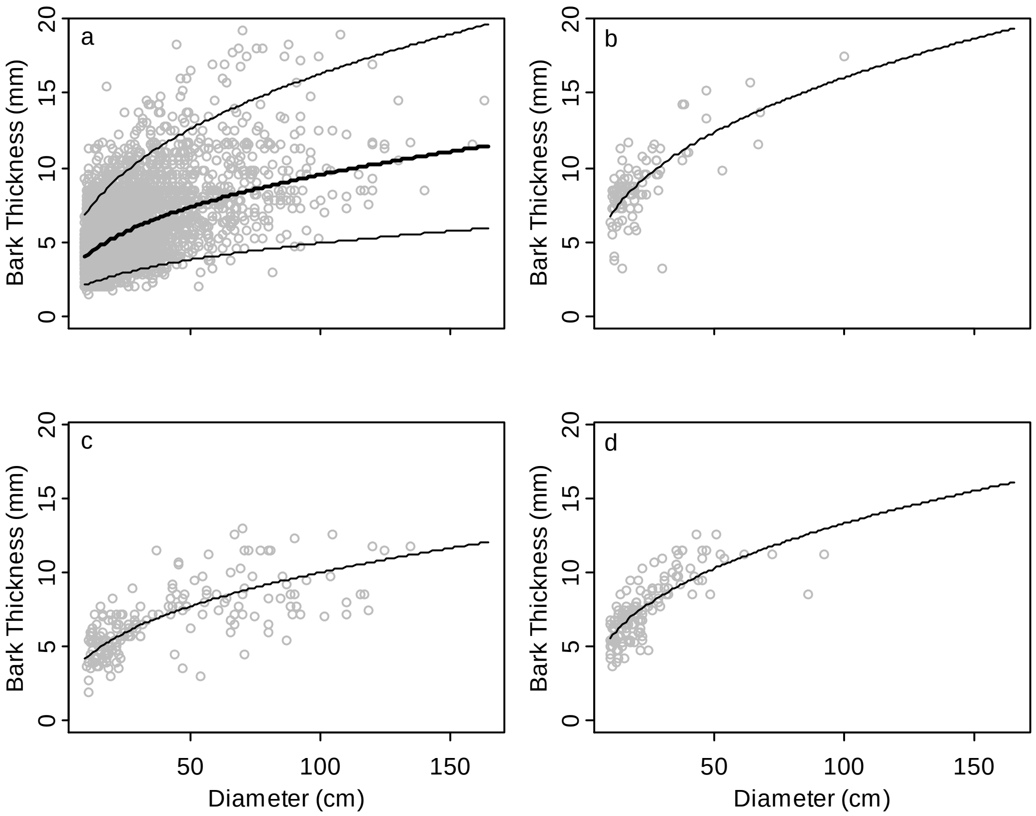

Figure 3.1. Bark thickness - diameter relationships for Ghanaian tree species. a) All species with log-log curves for species with the maximum, median (thick line) and minimum bark thickness. b-d) Species specific curves for *Entandrophragma angolense*, *Triplochiton scleroxylon* and *Ricinodendron heudelotii* respectively.

Table 3.2. ANOVA table for the linear regression model of bark thickness (log transformed) as function of *D* (log transformed) and species; n = 6569.

	df	Sum of Squares	Mean Square	F	*p*
log(D)	1	223.5	223.5	4560.3	< 0.0001
Species	163	373.3	2.3	46.7	< 0.0001
Residual	6404	313.8	0.05		

3.4.2 Impacts of fire on current structure and dynamics

After 15 - 27 years of regeneration since the most recent fire, the structure of some burnt forests remained substantially altered compared to unburnt forest plots in 2010, with past fire intensity score explaining much of the variation among plots (Fig. 3.2a, b). Both stem density and biomass decreased significantly with increasing fire intensity (stem density: F = 50.2, $p < 0.001$, $r^2 = 0.85$, biomass: F = 14.2, $p = 0.005$, $r^2 = 0.59$). In 2010, the most intensely burnt plot, ASU-88, had a stem density of just 182 stems ha^{-1} and biomass of just 137 Mg ha^{-1} compared to the unburnt plot mean stem density of 547 stems ha^{-1} and biomass of 324 Mg ha^{-1}. Overall, biomass values in 2010 were 127 - 382 Mg ha^{-1} in burnt plots and 299 - 350 Mg ha^{-1} in unburnt plots and stem densities in 2010 were 182 - 452 stems ha^{-1} in burnt plots and 500 - 639 stems ha^{-1} in control plots.

Forest dynamics in the post-fire period (1990 - 2010 for once burnt plots, 1995 - 2010 for twice burnt plots) were also significantly related to past fire intensity score. However, relationships were weaker than between forest structure and past fire intensity score. Both stem and biomass mortality rates increased with higher past fire intensity score (stem mortality: F = 13.88, $p = 0.006$, $r^2 = 0.59$, biomass mortality: F = 6.0, $p = 0.040$, $r^2 = 0.36$, Fig. 3.2d, g). When split between large (≥ 30 cm D) and small (< 30 cm *D*) trees, only post-fire stem mortality rates of small trees were significantly related to fire intensity (large stem mortality: F = 1.6, $p = 0.8$, $r^2 = 0.065$, small stem mortality: F = 19.74, $p = 0.002$, $r^2 = 0.68$, Fig. 3.2e). Despite this, there was no significant relationship between the current proportion of small trees (< 30 cm *D*) and past fire intensity score (F = 2.1, $p = 0.18$, $r^2 = 0.11$, Fig. 3.2c). The significant relationships between post-fire mortality rates and past fire intensity score appear to be driven by the very high mortality in plot ASU-88 which was twice burnt and had the highest fire intensity score; these relationships are not significant if this outlier is excluded. Post-fire stem recruitment and biomass growth rates both increased with past fire intensity score (stem recruitment: F = 12.8, $p = 0.007$, $r^2 = 0.57$, biomass growth: F = 7.0, $p = 0.030$, $r^2 = 0.40$, Fig. 3.2e, h). However, there was no significant relationship between past fire intensity score and post-fire biomass recruitment rates (F = 2.6, $p = 0.14$, $r^2 = 0.15$, Fig. 3.2i).

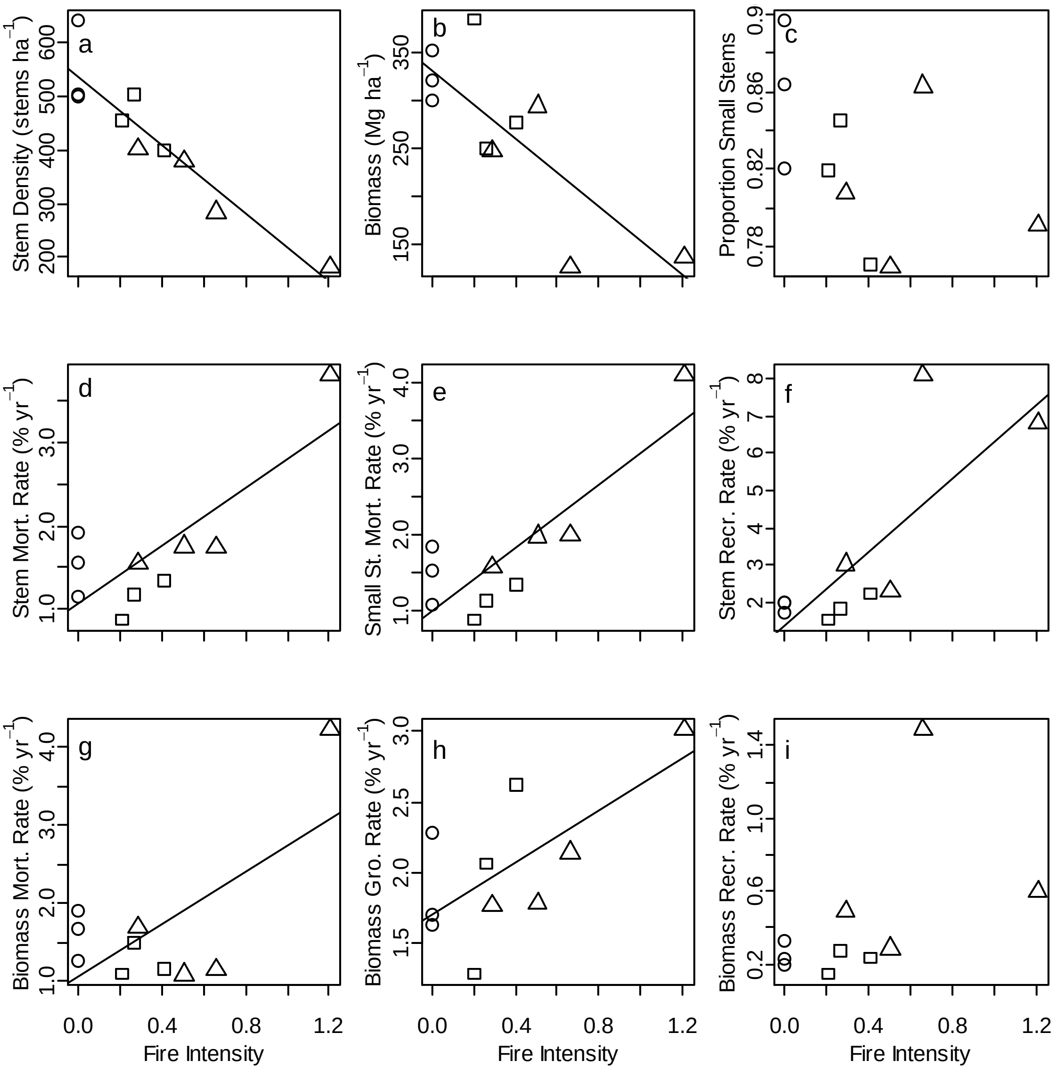

Figure 3.2. Relationship between past fire intensity score and structural and dynamics variables, 27 years after initial fires. Circles - unburnt, squares - once burnt plots (fire in 1983), triangles - twice burnt plots (fires in 1983 and 1995). Rates are calculated for post-fire periods, 1990 - 2010 for control and once burnt plots, and 1995-2010 for twice burnt plots. Regression lines are shown for significant results.

3.4.3 Impacts of fire on functional composition

The functional composition of forests in 2010 also varied with past fire intensity score (Fig. 3.3). The plots that had experienced the most intense past fires contained very high percentages of pioneer trees, and the relationship between past fire intensity score and percentage of pioneers was significant (F = 21.53, p = 0.002, r^2 = 0.70, Fig. 3a). The percentage of deciduous stems in 2010 increased with past fire intensity score (F = 8.7, p = 0.018, r^2 = 0.46, Fig. 3g) whilst mean wood density decreased with increasing past fire intensity score (F = 12.2, p = 0.008, r^2 = 0.56, Fig. 3h). The percentage of non-pioneer light demanders and understorey species in 2010 decreased with increased past fire intensity score (NPLD: F = 35.0, $p < 0.001$, r^2 = 0.79, understorey: F = 19.7, p = 0.002, r^2 = 0.67, Fig. 3.3b, d). Plot mean bark thickness (of a 20 cm *D* stem) significantly increased with past fire intensity score (F = 9.0, p = 0.017, r^2 = 0.47, Fig. 3.3i). No significant relationships were found between the percentage of shade-tolerants, sub-canopy or canopy species with past fire intensity score.

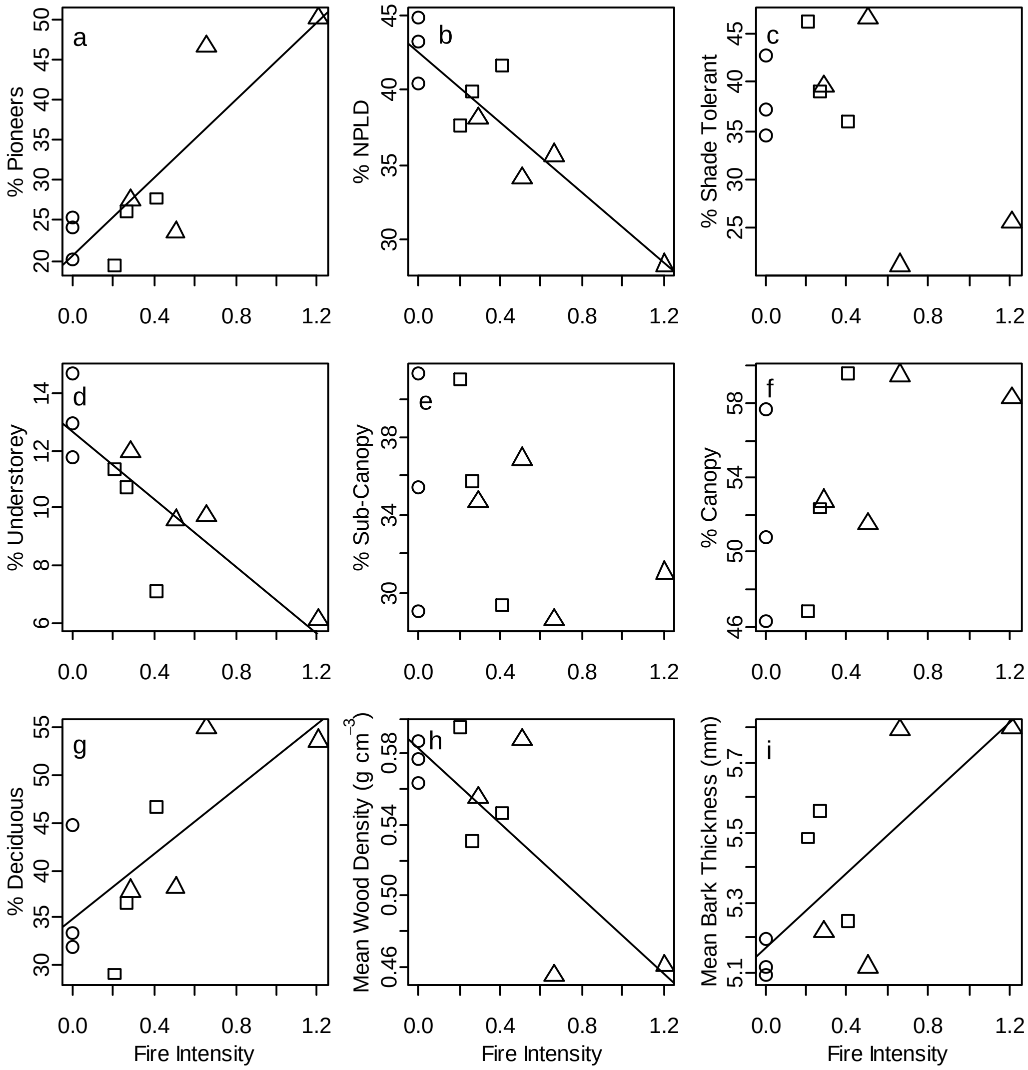

Figure 3.3. Relationships between functional composition and fire intensity in 2010, 27 years after initial fires. Circles - unburnt, squares - once burnt plots (fire in 1983), triangles - twice burnt plots (fires in 1983 and 1995). All percentages are arc-sine square root transformed. Regression lines are shown for significant results.

The majority of changes in functional composition with past fire intensity are due to post-fire regeneration of species with particular traits (Fig. 3.4). Post-fire recruitment of pioneer species increased with past fire intensity score (F = 51.9, $p < 0.0001$, $r^2 = 0.85$, Fig. 3.4a), and recruitment of non pioneer light demanders and shade-tolerant species decreased (NPLD: F = 37.2, $p = 0.0003$, $r^2 = 0.80$, shade-tolerant: F = 5.3, $p < 0.05$, $r^2 = 0.33$, Fig. 3.4b, c). Deciduous species showed increased post-fire recruitment (F = 12.9, $p = 0.007$, $r^2 = 0.57$, Fig. 3.4g) and mean wood density of post-fire recruits decreased with increased past fire intensity score (F = 23.5, $p = 0.001$, $r^2 = 0.71$, Fig. 3.4h). There were no significant patterns in either recruited or dead stems of understorey trees with past fire intensity score (Fig. 3.4d), despite a significant decrease in the percentage of understorey trees with past fire intensity (Fig. 3.3d). Recruited trees had thicker bark in more intensely burnt plots, whilst trees that died had thinner bark (recruits: F = 36.1, $p = 0.0003$, $r^2 = 0.80$, dead: F = 5.7, $p <=0.04$, $r^2 = 0.35$, Fig. 3.4i).

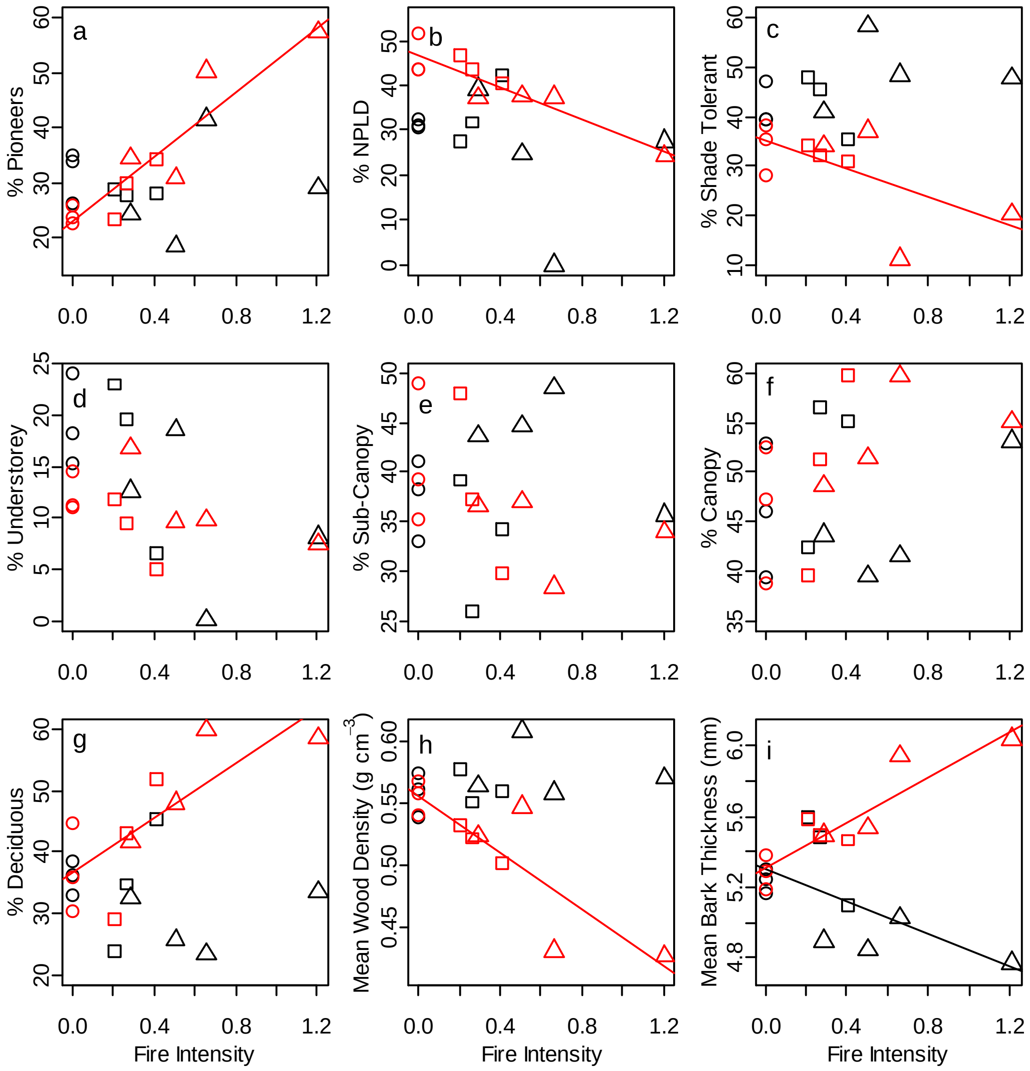

Figure 3.4. Patterns in functional composition of recruited trees (red) and dead trees (black) with fire intensity. Recruited and dead trees based on post-fire periods: 1990 - 2010 for control (circles) and once burnt plots (squares, fire in 1983), and 1995-2010 for twice burnt plots (triangles, fires in 1983 and 1995). All percentages are arc-sine square root transformed. Regression lines are shown for significant results.

3.4.4 Impacts of fires on floristic composition

As well as differences in functional composition due to fire intensity, floristic composition was significantly altered by fire (Fig. 3.5, Table 3.3). In Asukese, the most striking result is the large changes in the most intensely burnt plots, ASU-88 and ASU-99 (Fig. 3.5b), which had very high mortality and recruitment during the study period, when compared with the two less intensely burnt plots at that site. Within Bobiri, burnt forest had an altered composition when compared to unburnt forest, with the unburnt plots clustered together (NMDS, Fig. 3.5a), and all unburnt plots moved in the same direction over time along the NMDS axes. Multivariate ANOVA on floristic similarities confirms that past fire intensity score is a significant predictor of variation in floristic similarity among sites (Table 3.3). However, census date and differences between plots were also significant (Table 3.3). In Bobiri forest where it is possible to compare changes over time in floristic similarity between burnt and unburnt plots, an interaction term between census date and fire intensity was included in the multivariate ANOVA. The lack of significance of this term shows that burnt plots do not become more similar to unburnt plots over time, as with time there is no change to the impact of fire intensity on floristic similarity between plots.

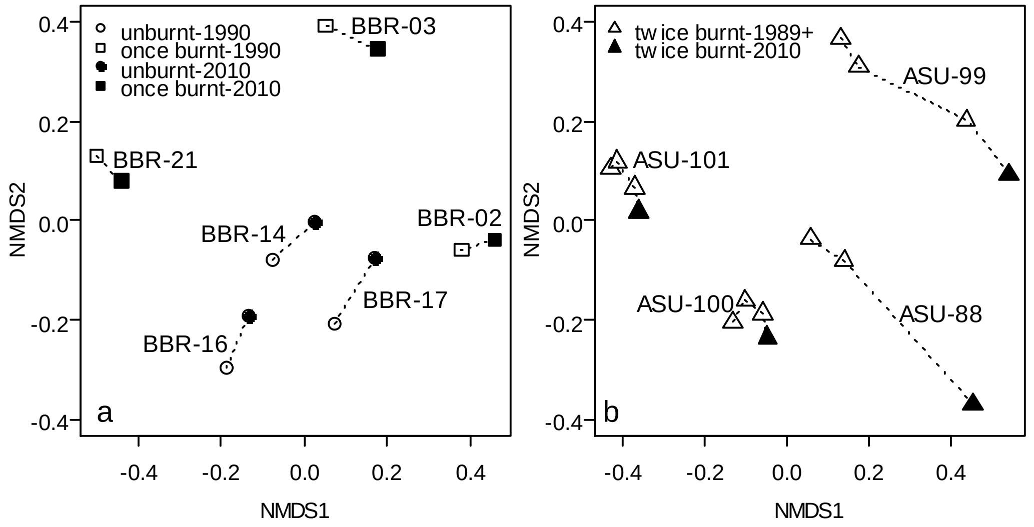

Figure 3.5. Ordination (non-metric multidimensional scaling using Hellinger distances) showing compositional trajectories of plots within a) Bobiri forest reserve and b) Asukese forest reserve. Circles - unburnt, squares - once burnt plots (fire in 1983), triangles - twice burnt plots (fires in 1983 and 1995). Filled symbols indicate the most recent census (2010). Previous censuses took place in 1990 only in Bobiri forest, and in 1989, 1995 and 2006 in Asukese forest (except 2006 in ASU-88).

Table 3.3. Multivariate ANOVA table based on a compositional similarity distance matrix using Hellinger distances from Bobiri forest and Asukese forest. Plot, fire intensity and census date all significantly explain variation.

Reserve	Variable	df	Sum of Squares	Mean Square	F	r^2	*p*
Bobiri	Date	1	0.03	0.03	3.5	0.03	0.007
	Fire Intensity	1	0.17	0.17	22.7	0.20	>0.001
	Plot	4	0.63	0.16	20.8	0.73	>0.001
	Date*Fire	1	0.007	0.007	0.86	0.008	0.574
	Residual	4	0.03	0.008			
Asukese	Date	1	0.15	0.15	8.1	0.04	>0.001
	Fire Intensity	1	0.30	0.30	16.0	0.20	>0.001
	Plot	2	0.87	0.43	23.3	0.73	>0.001
	Residual	10	0.19	0.02			

3.4.5 Impacts of fires on trajectory of stem density and biomass

The 1983 fires caused substantial loss of stems and biomass (Fig. 3.6). The estimated reduction of stems in burnt plots ranged from 15 - 78 % of the estimated mean unburnt plot stem density (503 stems ha^{-1}) in 1983. However, the burnt plots in both Bobiri and Asukese have since shown a consistent increase in stem density and on average have recovered 15 % of the initial estimated unburnt stem density (76 stems). This increase for the majority of burnt plots still has not replaced all the stems lost to the fires. However one plot, BBR-03, recovered stems sufficiently to match the 1983 control mean by 2010. Initial estimated biomass loss due to the 1983 fires was similar to stem density losses (Fig. 3.6b) ranging from 18 - 78 % of the estimated mean unburnt plot biomass (286 Mg ha^{-1}) in 1983, however, once burnt BBR-21 had 21 % higher biomass than the average control plot and the lowest fire intensity. All burnt plots gained biomass over the study period except ASU-88, which had the highest fire intensity. BBR-02 and ASU-100 recovered biomass to close to the 1983 control mean by the final census, while BBR-21 remained at high biomass throughout the study period. There is uncertainty associated with the precise values of the percentage losses presented here, as they are based on estimated values (see Section 3.3.9), however the general reductions and recovery patterns shown by each plot are valid.

The second fire in Asukese does not appear to have had a large impact on forest structure (Fig. 3.6). In all twice burnt plots, stem density was reduced immediately following the 1995 fires (Fig. 3.6a) and biomass decreased in three of the four twice burnt plots (Fig. 3.6b). However, the changes due to the second 1995 fire were much smaller in magnitude than the estimated losses due to the 1983 fires.

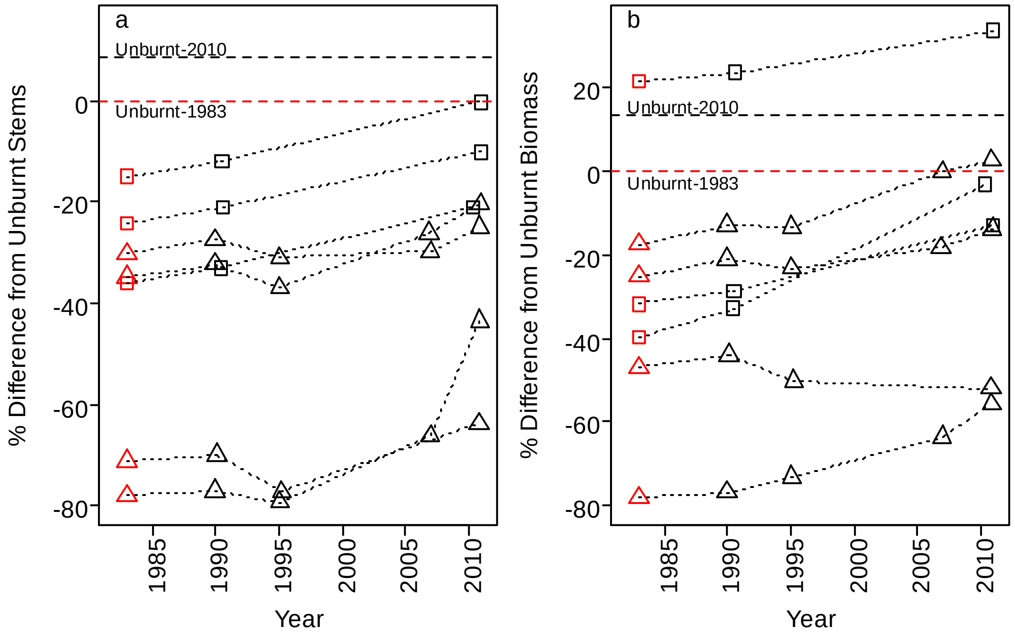

Figure. 3.6. Burnt plot stem density and biomass over the study period as a percentage of a) estimated 1983 mean unburnt plot stem density (503 stems ha^{-1}) and b) estimated 1983 mean unburnt plot biomass (286 Mg ha^{-1}). Dashed lines show the mean control stem density and biomass at 1983 and 2010 (stem density 2010: 547 stems ha^{-1}, biomass 2010: 324 Mg ha^{-1}). Squares - once burnt (fire in 1983), triangles - twice burnt (fires in 1983 and 1995). Dotted lines show the trajectory of plots over time. All data points for 1983 were estimated using recruitment, growth and mortality rates from the 1990 - 2010 census data (see Section 3.3.9) and are shown in red. Dashed lines representing 1983 mean unburnt plot stem density and biomass are also estimated and shown in red. Stem density and biomass of the majority of plots, both burnt and unburnt, increased over time.

3.5 Discussion

This study assesses 27 years of tropical forest regeneration from understorey fires and shows that understorey fires can have large impacts on forest structure and functional composition even after many years of recovery. Over the study period, forest structure showed evidence of recovery, however functional and floristic composition remained altered. Fire intensity score, measured retrospectively using char heights, was an excellent predictor of many structural, dynamic and compositional variables, showing the importance of this variable in the estimation of fire impacts on tropical forests.

3.5.1 Long-term fire impacts on forest structure

27 years after the initial 1983 fires, forest structure was still significantly altered in burnt forests (Fig. 3.2a, b) with lower stem densities and aboveground biomass in more intensely burnt forests. Stem density was as low as 182 stems ha^{-1} and biomass as low as 127 Mg ha^{-1} in the most intensely burnt plots when measured in 2010. Compared with the 2010 unburnt plot means, these reductions represent losses of 67 % of stems and 60 % of biomass. Current variation in forest structure among burnt plots is closely related to past fire intensity, showing the long-term impacts of fire on forest structure. However, forest structure variables and biomass in particular are not substantially reduced in once burnt plots in comparison to unburnt plots in 2010, with some plots showing similar or higher biomass and stem densities than unburnt plots (Fig 3.2). This result shows substantial recovery over the study period in these plots which experienced lower fire intensities (discussed further in Section 3.5.3). The magnitude of losses after 27 years for the most severely affected plots are similar to the only other comparable study, a chronosequence showing aboveground biomass 29 years after fire in a seasonally dry tropical forest in Mexico was still reduced by 57 % compared to mature forest biomass (Vargas *et al.* 2008).

3.5.2 Long-term fire impacts on functional and species composition

Even with 15 - 27 years of recovery, the functional and species composition of these forests remained altered compared to unburnt forests, and again this was closely linked to fire intensity. The results showed an increase in the proportion of pioneer species and traits associated with pioneer species (deciduousness, low wood density) with increasing past fire intensity (Fig. 3.3). This increase in pioneer species is due to the high percentage of recruited stems that were pioneer species over the post-fire study period (Fig. 3.4). This influx of pioneers is expected given the high mortality due to the fire event and has been observed in many other studies (Holdsworth & Uhl 1997; Cochrane & Schulze 1999; Gerwing 2002; Slik *et al.* 2002; Slik & Eichhorn 2003; Barlow *et al.* 2008; Slik *et al.* 2008; Slik *et al.* 2010). Pioneer species were still more abundant in burnt plots even after 15 - 27 years since the most recent fire and made up a large proportion of recruits, suggesting little evidence of recovery of the successional guild composition within the study period. However, Slik *et al.* (2008) showed that in Borneo plot mean wood density similarly declined over the first seven years of post fire regeneration based on the > 10 cm *D* size class, yet when based on small stems < 5 cm *D,* plot mean wood density increased (Slik *et al.* 2008). Regeneration of higher wood density, late successional species could have begun to occur in the burnt plots in this study, but this may have been obscured by measuring only stems ≥ 10 cm *D*.

The percentage of understorey trees declined with increasing past fire intensity (Fig. 3.3d). Unlike the increase in pioneer species, this does not appear to have been driven by selective recruitment or by mortality of understorey trees in the post-fire period (Fig. 3.4). Understorey species are likely to be small and therefore have thinner bark (Fig. 3.1, Paine *et al.* 2010), which increases susceptibility to fire-induced mortality (Uhl & Kauffman 1990; Barlow *et al.* 2003a, van Nieuwstadt & Sheil 2005; Brando *et al.* 2012, Slik *et al.* 2010). The higher fire-induced mortality of understorey trees during the 1983 and 1995 fire events may therefore still be visible in the burnt forest communities, and there does not appear to have been any preferential recruitment of understorey species over the study period.

Plot mean bark thickness increased with increasing past fire intensity (Fig. 3.3i). During the post-fire period, dying trees had lower bark thickness in plots with higher past fire intensity. This is driven by the twice burnt plots and is likely a result of delayed fire-induced mortality of thin barked trees from the 1995 fires. Interestingly, recruited stems had thicker bark in the burnt plots. This may be a result of the post-fire community containing a greater proportion of thicker barked species which subsequently reproduced over the study period. This finding has not been observed before, and may result in greater resilience of the forest to additional fires.

The clear differences in functional composition with past fire intensity show that the influence of fire on composition, and the patterns in recruitment over the study period show that forest functional composition is not reverting to a pre-fire composition during the first decades of recovery. The ordination analysis shows that over the study period, the composition of burnt plots did not become more similar to the unburnt plots. Overall, these results are comparable to those of other studies that suggest floristic composition does not revert to pre-fire composition within the first 15 years after fire (Slik *et al.* 2002; Barlow & Peres 2008).

3.5.3 Recovery trajectory of forest structure

Stem density and biomass were severely reduced due to the 1983 fires (Fig. 3.6). Stem density was reduced by 15 - 78 % in burnt plots compared with the estimated mean 1983 control stem density, within the wide range of values from other studies (8 - 90 %, Barlow & Peres 2006). Biomass was lost due to fire in six of the seven burnt plots, ranging between 18 - 78 %. One plot, BBR-21, had greater biomass than the estimated unburnt plot mean. The wide range of biomass losses found in this study have also been shown for other regions; Cochrane & Schultze (1999) recorded biomass losses of 20 - 90 % in burnt compared with nearby unburnt forests, all of which had been previously logged and Gerwing (2002) recorded biomass losses in logged forests of 32 % in lightly burnt areas and 68 % in heavily burnt areas compared with only logged forests. The precise values of stem density and biomass losses here should be treated with caution as they are based on estimated values using backwards projections of plot dynamic rates, rather than being based on pre-fire data for each burnt plot. However, the large variation in losses, which were severe in some areas, is a valid result.

Despite the large reductions in stems and biomass due the 1983 fires, all plots showed some level of recovery during the 27 year study period. The majority of burnt plots showed increased stem density and biomass over the study period (Fig. 3.6) associated with increased stem recruitment and biomass growth. As there are lower stem densities in burnt plots, recruitment and growth of surviving trees is likely to have increased compared to unburnt plots due to the reduced levels of competition. Other studies have shown increased regeneration of seedlings and saplings in burnt forests in studies up to 5 years post-fire (Swaine *et al.* 1997; Gould *et al.* 2002; Cleary & Priadjati 2005). Over longer post-fire periods evidence of regeneration of larger stems is also found. For example, seven years after fires in Borneo Slik *et al.* (2008) found increases in stem density of 5 - 10 cm and > 10 cm *D* size classes compared to 1.5 years post-fire. In addition, between three and nine years after fires in the Brazilian Amazon, high recruitment into the 10 - 20 cm *D* size class resulted in abundance of trees in this size class to approach the densities found in adjacent unburnt forests (Barlow & Peres 2008). Slik *et al.* (2002) also found density of stems > 10 cm D in burnt forests recovered to pre-disturbance levels within 15 years of fire in Borneo.

Although some studies have shown substantial impacts from repeated fires (Cochrane *et al.* 1999; Cochrane & Schulze 1999; Barlow & Peres 2008), the second fire in 1995 only had a small impact on forest structure in the twice burnt Asukese plots. Two plots in Asukese experienced high fire intensities and showed low stem density and biomass in 2010 (Fig. 3.2a, b). However, the stem density and biomass estimates of these plots were severely reduced even before the 1995 fires and the twice burnt plots displayed only small reductions in stem density and biomass after the 1995 fire (Fig. 3.6). Repeated annual fires in experimental burns showed reductions in flame height compared to the initial fire potentially due to a lack of fuel limiting forest flammability (Balch *et al.* 2008). This pattern was also found by Slik *et al.* (2008) in Borneo where there was a similar time period between the initial and second fires to this study. During the period between fires some of the woody debris produced during the first fire may have decomposed and the canopy may have closed, increasing the humidity of the understorey and reducing fire intensity (Slik *et al.* 2008).

These results show the potential for recovery of the structure of burnt plots. Given 27 years to recover from initial burning, with a second milder fire 12 years following the first in some cases, one plot reached the estimated 1983 unburnt plot stem density, and three plots reached biomass values similar to or greater than the estimated 1983 unburnt plot biomass (Fig. 3.6). These plots reaching similar biomass and stem density values to the unburnt estimates are primarily from once burnt sites, or twice burnt sites which had experienced low fire intensities. The two plots which experienced the highest fire intensities do not show any approach to unburnt plot values. However, as they also lost the most stems and biomass, this is not unexpected and there may be ecosystem limitations to the degree of recovery possible over a given time period. Furthermore, invasion by the exotic herbaceous weed *Chromolaena odorata* had occurred in the two most affected plots which may have further reduced potential recovery, especially tree recruitment in open canopy areas where the weed covered the ground in thick layer (pers. obs.).

To estimate the time required for all burnt plots to regain stems and biomass similar to the unburnt plots, the recruitment and mortality rates during the post-fire period (1990 - 2010 for once burnt plots and 1995 - 2010 for twice burnt plots) were used to model the trajectory of change over time in stem density and biomass starting from the estimated 1983 post-fire values. The models show that recovery of lost stems and biomass would take 15 - 70 years (Fig. 3.7). These are likely to be minimum estimates, particularly for the most severely affected plots; the early stages of regeneration over which the recruitment and dynamics rates are estimated are likely to also show the fastest recovery and may decrease over time.

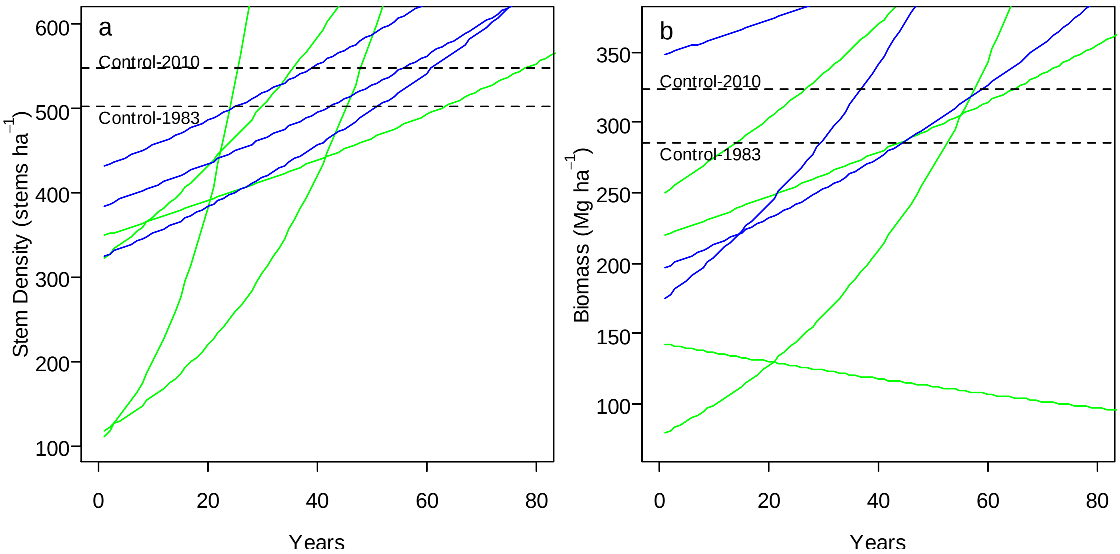

Figure 3.7. Modelled stem density (a) and biomass (b) trajectories of burnt plots from the initial fire. Once burnt plots - blue, twice burnt plots - green. Dashed lines show the mean estimated unburnt plot stem density and biomass for 1983 and 2010. Recruitment and mortality rates during the post-fire period (1990 - 2010 for once burnt plots and 1995 - 2010 for twice burnt plots) were applied to the 1983 estimated post-fire stem density and biomass values.

This study is limited by complications that arise from the lack of pre-fire data at the study sites and the comparison of burnt plots with adjacent unburnt areas. This problem is faced by the majority of studies in this field that use natural fire events rather than experimental burns (e.g. Cochrane & Schulze 1999; Gerwing 2002; Slik & Eichhorn 2003; Barlow & Peres 2004; Slik *et al.* 2008). It is not possible to prove that the burnt plots included in this study were identical to the unburnt plots before the fires, but the finding that the fire intensity score closely relates to forest structure (Fig. 3.2a, b) suggests the fire rather than other factors has resulted in the current differences in structure. Furthermore, the control and burnt plots are all located in the same forest type with similar total rainfall, seasonality and soils. The census interval used for analyses of the twice burnt plots (1995 - 2010) is also a complication as it may include some delayed fire-induced mortality, as mortality is typically high for three years following fires (e.g. Barlow *et al.* 2003b). This is likely the cause of the increased mortality found with increased fire intensity (Fig. 3.2d, g, e).

3.5.4 Improving modelling and emissions estimates of tropical understory fires

This study and others (Cochrane & Schulze 1999; Barlow *et al.* 2003a; Barlow & Peres 2004; Balch *et al.* 2011; Brando *et al.* 2012) show the importance of fire intensity for understanding the impacts on forest structure and the wide variation in intensity within a single burnt area. However, integrating this insight into remote sensing and modelling of tropical forest understorey fires is challenging. Combining burnt area mapping with higher-resolution methods could be used to improve estimations of fire-impacts on vegetation and emissions estimates (e.g. Numata *et al.* 2011). Improvements in tropical forest fire modelling to include variation in fire behaviour, such as the development of models to predict forest flammability, and incorporating vegetation models to include post-fire regeneration will aid the prediction of future impacts of understorey fires (e.g. Soares-Filho *et al.* 2012).

This study assessed the impacts of historic fires on forest structure and composition, 27 years after the first fire event. This is considerably longer than the time periods assessed by other studies. Even after 27 years since initial fires, biomass and stem density was still significantly altered in some plots whilst others showed substantial recovery reaching unburnt plot values. The intensity of past fires contributed to current variation in structure and functional composition. In addition, the results support the few previous long-term studies which show evidence of regeneration of forest structure during the years following forest fires, but still little recovery of species composition. Given the observed regeneration of forest structure, this study supports the notion that fire-disturbed forests still have conservation value (Slik *et al.* 2002) and continue to provide ecosystem services. In the long-term, if left to regenerate, these fire-disturbed forests could be valuable, especially in areas of high fragmentation and few remaining natural stands such as West Africa. However, with the likely increasing fire occurrence in tropical forests due to fragmentation, logging and climate change, prevention of wildfires should be given a high priority.

4. Spatial and temporal trends in liana infestation in Ghanaian tropical forests

4.1 Abstract

Studies of recent changes in the abundance of lianas in tropical forests have yielded varying results: work in Neotropical forests has shown an increase, whereas the small number of studies from African forests have tended to show decreases in liana abundance. These results highlight that the drivers of liana increase are unknown, with proposed hypotheses including increased natural disturbance, land use change, elevated temperatures and increased atmospheric CO_2. Studying the drivers of liana spatial distribution and change in liana abundance at the same location may increase our understanding of the causes of these patterns. Here there is the opportunity to test for change in liana abundance (measured using liana infestation rates) and the drivers of the spatial patterns of liana abundance in the forest zone of Ghana. The results show a very slight but significant increase in the percentage of trees carrying lianas from 78.6 % (± 13.9 sd) in the early 1990s (mean census date 1991.84) to 81.2 % (± 15.1 sd) in the late 2000s (mean census date 2008.91). Liana spatial distribution was driven by variation in forest structure rather than precipitation or soil properties. However the observed changes in liana infestation over time could not be explained by changes in forest structure over the same period. Large lianas (≥ 10 cm diameter) display different relationships with environmental variables to the liana community as a whole, with higher abundance in sites with lower turnover rates. In conjunction with the results from other studies, these findings suggest that changes in liana abundance may be landscape-specific, and we should not necessarily expect a simple global driver or trend.

4.2 Introduction

One of the most compelling patterns to emerge from recent studies of long-term change in tropical forests is an increase in liana (woody vine) abundance in the Neotropics (Schnitzer & Bongers 2011). This result was first reported by Phillips *et al.* (2002) who showed an increase in the abundance of lianas ≥ 10 cm diameter since the 1980s in permanent sample plots in Amazonia. This finding has been supported by studies from Barro Colorado Island (BCI), Panama, which have shown an increased production of liana leaf litter (Wright *et al.* 2004) and flowers (Wright & Calderon 2006) since the mid 1980s, and an increased percentage of trees infested with lianas since 1967 (Ingwell *et al.* 2010). In addition, a small increase in stem numbers and biomass of lianas ≥ 10 cm diameter was found over a 10 year period in French Guiana (Chave *et al.* 2008b). However, not all studies find this pattern. For example, there was a 20 % decrease in liana stem density between 1979 and 1992 in 1.6 ha of Gabonese forest (Caballé & Martin 2001), whilst in the Democratic Republic of Congo liana stem density decreased by 33.5 % between 1994 and 2007 in two 10 ha plots (Ewango 2010). Overall, more studies are needed to understand whether the temporal trend in liana abundance is consistent across tropical forests.

Any changes to the abundance of lianas are important, not only because lianas are a key part of tropical forest ecosystems as they contribute approximately 25 % of woody species richness (Gentry 1991), but also because of the negative impact of liana infestation on tree hosts. Lianas decrease tree growth (Clark & Clark 1990; van der Heijden & Phillips 2009a; Ingwell *et al.* 2010) and increase tree mortality (Putz 1984a; Phillips *et al.* 2005; Ingwell *et al.* 2010). Therefore, understanding liana ecology is important for understanding tropical vegetation dynamics and the carbon storage and sequestration potential of tropical forests. There have been many hypotheses proposed to explain the increase in liana abundance in the Neotropics such as increased evapotranspiration demand, increased rates of natural disturbance, land use change and elevated atmospheric CO_2 (Schnitzer & Bongers 2011). However, the current lack of evidence for an increase in liana abundance in African forests raises questions about whether this trend can be explained by any single driver. For example, some possible drivers, such as elevated CO_2 or increased evapotranspiration demand due to increased temperatures, might be expected to affect all tropical forests. In contrast, the variation in changes in liana abundance in different forests suggests that the drivers are likely to be a complex combination of these global trends interacting with local conditions (Schnitzer & Bongers 2011). Therefore, we need to assess temporal patterns in liana abundance in the context of the landscape in which they occur. Assessing temporal patterns of liana infestation in combination with local drivers of liana spatial distribution may aid our understanding of the drivers of change over time.

Over different scales climate, forest structure, disturbance and soil fertility have all been proposed as drivers of liana spatial distribution. As lianas are climbing plants that use host trees to reach the canopy, forest structure and host availability have been suggested as determinants of liana distribution (Putz 1984a) and forest structural variables have been found to be significant predictors of liana abundance in many studies (Putz 1984a; Balfour & Bond 1993; Laurance *et al.* 2001; Nabe-Nielsen 2001; Phillips *et al.* 2005; van der Heijden & Phillips 2008; Nogueira *et al.* 2011). Lianas may also be favoured by forest disturbance such as tree fall events (Schnitzer & Bongers 2002) as they have the capacity to survive the disturbance and subsequently resprout in canopy gaps (Putz 1984a; Fisher & Ewers 1991) and can grow horizontally into gaps from the forest floor (Penalosa 1984). Consistent with these mechanisms, liana abundance and species richness have been found to increase with forest disturbance (Laurance *et al.* 2001; van der Heijden & Phillips 2009b), in tree fall gaps (Gerwing & Farias 2000; Schnitzer *et al.* 2000) and at forest edges (Laurance *et al.* 2001). Patterns of soil fertility may also control liana spatial distribution; lianas may increase in abundance in forests with greater soil fertility due to the high resource demand of their extensive, nutrient rich and high turnover foliage (Zhu & Cao 2010). Significant, though typically weak, relationships between liana abundance and soil chemical and physical properties have been observed, such as a positive correlation with soil fertility (Putz & Chai 1987; Laurance *et al.* 2001; Phillips *et al.* 2005). However, the relationship between liana abundance and climate is less clear. Schnitzer (2005) provides a compelling case for liana abundance to increase with lower rainfall and increased seasonality. The physiology of lianas, with deep roots systems and long, wide xylem vessel elements, make them particularly effective at water uptake, and as such may provide a competitive advantage over trees during periods of water stress (Schnitzer 2005; Zhu & Cao 2009). Evidence has been found to support the hypothesis that liana abundance (or liana species richness) is favoured by water stress (Schnitzer 2005; Swaine & Grace 2007; DeWalt *et al.* 2010; Toledo 2011), but other studies find either no effect, a weak effect or even an increase in liana abundance with increased precipitation (van der Heijden & Phillips 2008; van der Heijden & Phillips 2009b; Hu *et al.* 2010).

The drivers of liana distribution remain uncertain, particularly with regard to water stress, and there is a scarcity of studies assessing a range of different drivers simultaneously. Furthermore, understanding the importance of different drivers of liana distribution in a given landscape may provide a framework for understanding temporal changes in that region. Such studies are lacking in the literature as there are few datasets with historical information on liana abundance that can be extended with contemporary measurements. By utilising a widespread network of permanent sample plots established in Ghana during the early 1990s, a unique opportunity arose to assess both temporal changes in liana abundance over a decadal time-scale and determine the drivers of liana spatial distribution across the same study area. Using this data this study will test: 1) if liana abundance has changed over time, and 2) whether precipitation, forest structure, disturbance or soil properties drive liana spatial distribution (Table 4.2).

4.3 Methods

4.3.1 Study Sites

Forest inventory data were collected from a network of 19, one ha long-term permanent sample plots from ten forest reserves located within wet evergreen, moist evergreen and moist semi-deciduous forest habitat types in Ghana (Table 1.3, Hall & Swaine 1976; 1981). Recent long-term annual precipitation for each plot ranged from 1288 to 1928 mm yr^{-1} (Hijmans *et al.* 2005). Rainfall is highest along the south-west coast and decreases inland. The rainfall pattern is bimodal; the main dry season (months < 100 mm precipitation) begins in November or December and ends in February, with an additional dry month at all sites in August.

Plots were established by the Forestry Commission of Ghana (FCG) during the early 1990s in unlogged forests and were re-censused in the late 2000s as part of the current study (Table 1.3). Most plots remained undisturbed by humans during the study period. However, in eight plots some subplots (covering 0.04 - 0.48 ha per plot) had been affected by tree felling; these subplots were removed from the dataset. All plots were located at least 150 m from the nearest forest edge, with the majority at least 1 km within a reserve; fragmentation effects are typically found within 100 m of the forest edge (Laurance *et al.* 1998; 2001) and as such should not influence our analyses. None of the plots included in the study were known to have been burnt and at each site this was confirmed by examination of tree bases for evidence of fire scars. Although the precise long-term disturbance history of these plots is unknown they can all be considered to occur in old growth forest reserves, the majority of which were designated before 1940 (with the exceptions of Cape Three Points and Dadieso, established 1950 and 1977 respectively). Two plots previously separated on the basis of soil type were combined (Lewis *et al.* 2009a). Additional data from two, one ha permanent sample plots at the University of Ghana Kade Agricultural Research Station (Swaine *et al.* 1987) censused during 2010 were also included in the analysis of liana spatial distribution.

4.3.2 Measurements

Initial plot set-up and measurements were performed following Alder & Synnott (1992) and re-measurements followed similar standard protocols (Phillips *et al.* 2009b). Each tree stem ≥ 10 cm D (diameter at breast height; 1.3 m or above buttresses) was given a metal reference tag, and D and species identity was recorded. Following standard protocols (Phillips *et al.* 2009b), in the final censuses climbing lianas were included if they reached ≥ 10 cm at any point below 2.5 m height from the ground and diameter measurements were taken at three locations: 1.3 m from the ground, 1.3 m from the last rooting point, and the largest diameter below 2.5 m height from the ground (*Dmax*).

Within each plot, every tree included in the census was given a liana infestation score between 0 (no lianas present in tree) and 3 (tree heavily infested with lianas). This score was applied in both the initial and final censuses. As the score is subjective, during the 2009 and 2010 recensus only one individual (K.P. Duah) gave the score for all trees, and to assess temporal changes, this score was reduced to a binary measurement of 0 (uninfested) or 1 (infested) as multiple different observers gave the liana infestation scores for initial censuses of the plots. For the Kade plots the liana infestation scores were recorded during the final census only.

Additional liana surveys were carried out during the final censuses in 15 plots. 50 trees per plot were selected randomly, stratified by *D*; equal numbers of trees were sampled throughout the plot from each of five diameter size classes (10 - 19.9 cm, 20 - 29.9 cm, 30 - 39.9 cm, 40 - 49.9 cm, ≥ 50 cm). For each selected tree, all lianas entering the crown from the ground or adjacent tree crowns were counted in 10 mm size categories using either a calliper or visually estimating the size of lianas entering from adjacent crowns (van der Heijden *et al.* 2010).

4.3.3 Liana spatial abundance metrics

Five plot-level metrics of liana abundance were used to assess drivers of liana spatial distribution based on data collected in the most recent census: the percentage of trees infested, mean infestation score, number of large lianas (≥ 10 cm *Dmax*), liana stem number index and liana basal area index.

Liana stem number index and liana basal area index were calculated for each plot based on the liana survey data of 50 trees per plot. As the number and basal area of lianas infesting a tree are known to increase with host tree size (Clark & Clark 1990; Pérez-Salicrup & de Meijere 2005), host tree basal area was used to scale the measures of liana stem number and liana basal area in each sampled tree before calculating a plot-level index. Liana stem number index, *X*, of plot *p*, was estimated as

$$X_p = \sum_{i=1}^{S_p} \frac{X_i}{Z_i}$$

where *S* is the number of tree stems included in the liana survey (normally 50), X_i is the total number of liana stems infesting tree *i*, and Z_i is the basal area of tree *i*. Similarly, liana basal area index, *Y*, of plot *p*, was estimated as

$$Y_p = \sum_{i=1}^{S_p} \frac{Y_i}{Z_i}$$

where Y_i is the sum of basal areas of all lianas infesting tree *i*. In instances where S_p was less than 50, X_p and Y_p were adjusted to account for the number of trees included, i.e. X_p corrected = $(X_p / S_p) \times 50$.

4.3.4 Environmental variables

To test the importance of different hypothesised drivers of liana abundance, data for a suite of biotic and abiotic explanatory variables were assembled (Table 4.1).

Table 4.1. Environmental variables included to test the importance of different drivers of liana spatial distribution.

Hypothesised Driver	**Variable(s)**	**Reference for Hypothesis**
Precipitation	Mean annual precipitation (MAP)	Schnitzer *et al.* (2005)
Forest Structure	Stem density, basal area to stem ratio	Putz (1984a); Balfour & Bond (1993)
Disturbance	Turnover rate	Putz (1984a); Schnitzer & Carson (2001)
Soil properties	Principal component axes of soil variation	Putz & Chai (1987)

Mean annual precipitation (MAP, mm yr^{-1}), maximum cumulative water deficit (MCWD, mm, Aragão *et al.* 2007), a measure of seasonal drought stress, and dry season length (DSL, number of consecutive months < 100 mm precipitation) were derived from WorldClim (Hijmans *et al.* 2005). However, as MCWD was very strongly correlated to MAP (r = 0.92), and DSL at the sites varied between only 3 and 4 months, only MAP was included in analyses.

Plot-level forest structure variables included in the analyses of liana spatial distribution were tree stem density (stems ha^{-1}) and basal area to stem ratio (m^2 stem^{-1}: plot basal area divided by plot stem density). These variables were chosen as tree stem density provides an estimate of the number of potential hosts for lianas, and basal area to stem ratio provides an indication of the proportion of basal area made up by small trees which may provide climbing trellis for lianas to access the canopy.

Tree stem turnover was used as an indicator of natural disturbance caused by mortality and recruitment over the census period. Turnover rate is the mean of mortality and recruitment rates (Phillips & Gentry 1994) which were calculated following the equations presented in Lewis *et al.* (2004).

Soil cores were collected from each site and samples from 3 depths (0 - 5 cm, 5 - 10 cm and 10 -20 cm) were analysed for chemical and physical properties. For the majority of plots, laboratory analysis was carried out on only one soil core, and mean soil property values were calculated across the three depths. For plots within Asenanyo and Cape Three Points forest reserves, up to five cores per plot were analysed. Plot-level average values were calculated for each depth, and then across the three depths. No soil was available from plots within Dadieso forest reserve. Soils were analysed for pH, particle size, C:N ratio, concentrations of exchangeable ions, effective cation exchange capacity and total P following Quesada *et al.* (2010).

To assess pH, 10 g soil were shaken with 25 ml of H_2O for one hour, and allowed to rest for one hour. The pH of the supernatant was measured using an electronic probe.

Particle size fractions of sand (50 - 2000 μm), silt (2 - 50 μm) and clay (< 2 μm) were determined using the pipette method. 10 g of soil were mixed with 100 ml of H_2O and 20 ml of 5 % sodium hexametaphosphate, $(NaPO_3)_6$ (Calgon), and left overnight to disperse the clay. The solution was then mixed vigorously for 10 minutes in a commercial blender and the sand fraction removed using a 53 μm sieve. The remaining solution was poured into a 1 l measuring cylinder and mixed with a plunger. The solution was left for 3 - 4 hours depending on the temperature of the solution, and a 20 ml sample was removed from 5 cm below the surface using a pipette to provide a sample containing 1/50 of the clay fraction. The sand and clay fractions were dried at 105°C and weighed. The sand fraction was placed in the furnace at 500°C to remove any remaining organic matter and reweighed. The silt fraction was calculated as the initial weight minus the sand and clay fractions.

To determine percentages of total carbon and nitrogen 45 μg of soil were combusted at 1000°C and read by an automated elemental analyser. C:N ratios were then calculated.

Concentrations of exchangeable Al, Ca, K, Mg and Na were estimated using the silver thiourea (Ag-TU) extraction method (Pleysier & Juo 1980). 5 g of soil and 30 ml of Ag-TU were shaken for 4 hours, centrifuged for 15 minutes and filtered through Whatman 43 filter papers. Ion concentrations of extracts were determined using ICP-OES (inductively coupled plasma optical emission spectroscopy). Effective cation exchange capacity (ECEC) was calculated as the sum of concentrations of Al, Ca, K, Mg and Na.

For analysis of total phosphorus 0.5 g soil was digested in concentrated sulphuric acid (H_2SO_4) and additions of hydrogen peroxide (H_2O_2) (Tiessen & Moir 1993). Phosphorus concentration was determined using the ICP-OES.

All soil properties were included in a principal components analysis to identify the main axes of variation of soil properties for inclusion in the analysis of liana abundance. Soil variables which did not conform to the assumptions of a normal distribution were first appropriately transformed. The first three axes accounted for 79.4 % of the variation (Table 4.2, Fig. 4.1). Variables with high loadings on the first axis (PC1) were effective cation exchange capacity, exchangeable Ca and % N; higher values along this axis represent higher soil fertility. The second axis (PC2) was dominated by exchangeable Na and pH. Higher values along this axis represent lower pH and higher Na. The third axis

(PC3) is predominately controlled by particle size. High values along this axis represent high sand content and low clay content.

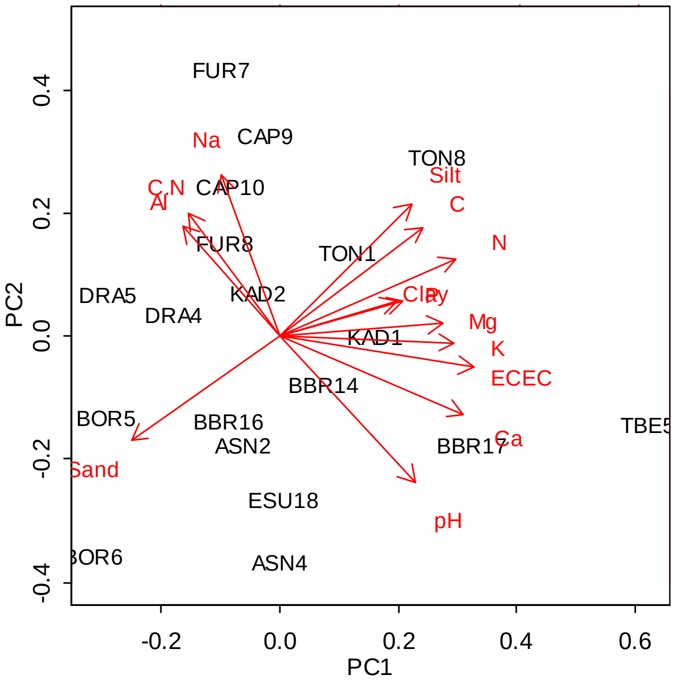

Figure 4.1. Biplot of PCA axes 1 and 2 with soil variables (red) and plots (black).

Table 4.2. PCA axis loadings of soil variables (with transformations indicated) and variance explained by each axis. Variables with high loadings for each axis are shown in bold.

Soil Variables	PCA Axes		
	1	2	3
1/(1-pH)	0.252	**-0.403**	0.085
% Sand	-0.279	-0.287	**0.336**
% Clay	0.217	0.096	**-0.509**
% Silt	0.245	**0.368**	-0.069
% N	0.328	0.216	0.200
% C	0.266	0.303	0.329
C:N	-0.171	0.339	**0.475**
√Al	-0.181	0.305	-0.335
Ca	**0.343**	-0.217	0.149
ln(K)	0.326	-0.018	0.063
Mg	**0.303**	0.036	0.135
Na	-0.111	**0.446**	0.139
ECEC	**0.362**	-0.086	0.072
ln(Total P)	0.228	0.096	-0.246
Proportion Variance Explained	0.47	0.20	0.13
Axis Definition	Soil fertility	Na, pH	Particle size

4.3.5 Data Analysis

The proportion of trees infested, an indirect measure, was used to assess change over time in liana abundance, as no direct measures of abundance were available for the historical censuses. This indirect measure of liana abundance correlates well with two more direct measures of liana abundance available from the 2009 and 2010 surveys: liana basal area index (r = 0.75, t = 4.04, df = 13, p = 0.0014) and liana stem number index (r = 0.65, t = 3.09, df = 13, p = 0.0086). Logistic regression within a mixed-effects modelling framework with nested random factors was used to test if time (a fixed effect) was a significant predictor of the probability of a tree being infested with one or more lianas. As this is an individual based analysis and some trees were given a liana infestation score twice (during the first and last census), individual was included in the model as a random factor nested within plot, nested within forest reserve. The Kade plots were excluded from this analysis as historical liana infestation data were unavailable.

To assess the relationships between the liana abundance metrics (percentage of trees infested, mean infestation score, number of large lianas, liana stem number index and liana basal area index) and climate, forest structure, turnover and soil variables, simple correlations and multiple mixed-effects models were used. Reduced datasets were used excluding plots without data for particular variables (six plots lack liana stem number index and liana basal area index data, and two plots lack soil data). Tree turnover rates and the number of large lianas were log transformed and percentage of trees infested was arc sine transformed prior to analysis. As many correlations were performed on the same dataset, Hochberg sequential Bonferroni adjustment (Hochberg 1988) was applied to the results to prevent Type I errors. To assess relationships between each liana metric and all environmental variables in a single analysis, a multi-model selection procedure was used. A mixed-effects modelling framework was used with reserve as a random factor. Models were estimated using maximum likelihood (ML) rather than restricted maximum likelihood (REML) in order to compare models with different fixed effects (Bolker *et al.* 2009). As tree stem density and basal area to stem ratio were correlated, and MAP and PC1 were correlated, four different multiple mixed-effects models were tested using each possible combination of the correlated variables, and for each different liana metric. Stepwise model selection based on the second order Akaike Information Criterion (AICc), which penalises model complexity and is appropriate for small sample sizes (Burnham & Anderson 2004), was used to arrive at the best models for each liana abundance metric. Response variables in both correlations and mixed-effects models were weighted by plot size. All data analysis was carried out in R (R Development Core Team 2012), using the package MuMIn (Bartoń 2012) for model selection.

4.4 Results

4.4.1 Change in liana infestation over time

Liana infestation status (infested or uninfested) was available for 10,121 individual trees and was measured on 16,024 occasions; 5093 trees were measured twice. Initial liana plot-level infestation rates were high: on average 78.6 % (± 13.9 sd, Fig. 4.2) of trees were infested during the first census (mean date 1991.84). By the end of the study period (mean date 2008.91), infestation rates had increased very slightly to 81.2 % (± 15.1 sd, Fig. 4.2). The logistic mixed-effects model (including nested random effects of reserve, plot and individual) showed that the probability a tree carried a liana significantly increase over time (Hosmer-Lemeshow statistic = 1714, $p < 0.0001$), though this effect was very slight. For example, the probability of infestation in plot BBR-14, with median random effect size, was estimated to have increased by only 0.18 % yr^{-1} over the 20 year study. Of the trees that survived the study period and therefore were measured twice, 52.1 % that were initially uninfested became infested by the end of the study period. Of the individuals that initially carried at least one liana, 11.4 % had become liana-free by the end of the study period.

The initial census infestation rates of dead trees (infestation recorded prior to death) and surviving trees, and the final census infestation rates of surviving trees and recruited trees are significantly different (F = 4.0, df = 3, $p = 0.01$, ANOVA, Fig. 4.3). Post-hoc analysis of the differences show that recruited trees have significantly higher infestation rates than trees that survived from the initial census (z = -3.3, $p < 0.005$) but differences between other categories were not significant, again showing that only small changes in infestation rates occurred over the study period.

Table. 4.3. Rates of liana infestation at the initial and final censuses and liana abundance metrics for each plot. - indicates no data available.

Forest Type	Plot Code	Plot Area (ha)	Infestation (%)		Mean Infestation Score	Lianas ≥ 10 cm *Dmax* (ha^{-1})	Liana Basal Area	Liana Stem Number	Soil Data Available
			Initial	Final					
Moist Semi-deciduous	ASN-02	0.6	91.8	92.6	1.95	23.3	-	-	Yes
	ASN-04	0.88	91.0	86.8	1.79	10.2	-	-	Yes
	BBR-14	0.88	83.7	83.6	1.61	6.8	2.20	1.37	Yes
	BBR-16	0.92	87.3	88.4	1.69	5.4	3.92	1.55	Yes
	BBR-17	0.96	81.8	82.1	1.66	8.3	1.97	2.30	Yes
	ESU-18	0.52	92.6	89.2	1.77	5.8	4.15	3.09	Yes
	KAD-01	1	-	87.2	1.70	10	4.32	1.87	Yes
	KAD-02	1	-	92.1	1.74	5	4.08	2.36	Yes
	TBE-05	0.64	80.3	85.2	1.66	4.7	2.86	2.18	Yes
Moist Evergreen	BOR-05	1	56.4	57.3	1.07	5	2.03	0.75	Yes
	BOR-06	1	68.6	97.3	2.04	17	4.29	2.01	Yes
	DAD-03	1	99.0	98.3	2.01	8	-	-	No
	DAD-04	1	93.4	95.0	1.85	7	-	-	No
	TON-01	1	65.6	70.5	1.39	9	1.45	1.36	Yes
	TON-08	1	79.9	88.0	1.87	5	2.96	1.93	Yes
Wet Evergreen	CAP-09	1	53.1	43.0	1.19	43	-	-	Yes
	CAP-10	1	54.6	60.7	0.72	4	-	-	Yes
	DRA-04	1	93.4	95.0	1.57	14	3.50	1.62	Yes
	DRA-05	1	66.7	85.1	1.16	9	2.55	1.52	Yes
	FUR-07	1	86.4	87.5	1.67	7	4.27	2.38	Yes
	FUR-08	0.6	82.2	89.4	1.70	6.7	3.50	2.36	Yes

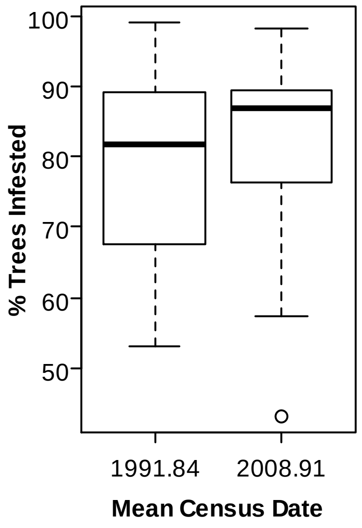

Figure 4.2. Percentage of trees infested across all plots at the initial and final censuses. Box - interquartile range, thick line - median, whiskers - range, circles - outliers.

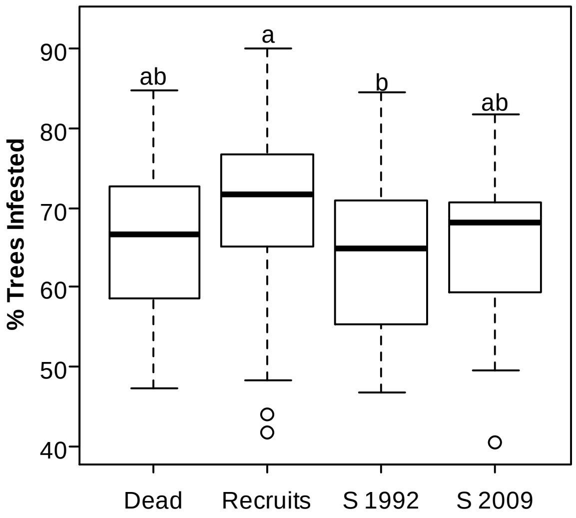

Figure 4.3. Differences in infestation rates between dead trees (infestation at initial census), recruited trees (infestation at final census), and surviving trees at the initial (mean date 1991.84) and final (mean date 2008.91) censuses. Box - interquartile range, thick line - median, whiskers - range, circles - outliers. Categories with the same letter are not significantly different from each other.

4.4.2 Correlations of liana abundance and environmental variables

After application of the Hochberg sequential Bonferroni correction, only one correlation between the liana abundance metrics and environmental variables was significant: liana basal area index was negatively correlated with tree basal area to stem ratio (r = -0.85, *p*

= 0.0001, Fig. 4.4e). Four correlations were significant at the $\alpha = 0.05$ level; liana basal area index increased with tree stem density (r = 0.58, *p* = 0.025), liana basal area index decreased with concentration of K (r = -0.55, *p* = 0.035), and both the percentage of trees infested and the mean liana infestation score decreased with concentration of Na (r = -0.51, *p* = 0.026 and r = -0.54, *p* = 0.017, percentage infestation and mean infestation score respectively). Mean annual precipitation was not significantly correlated with any liana metric.

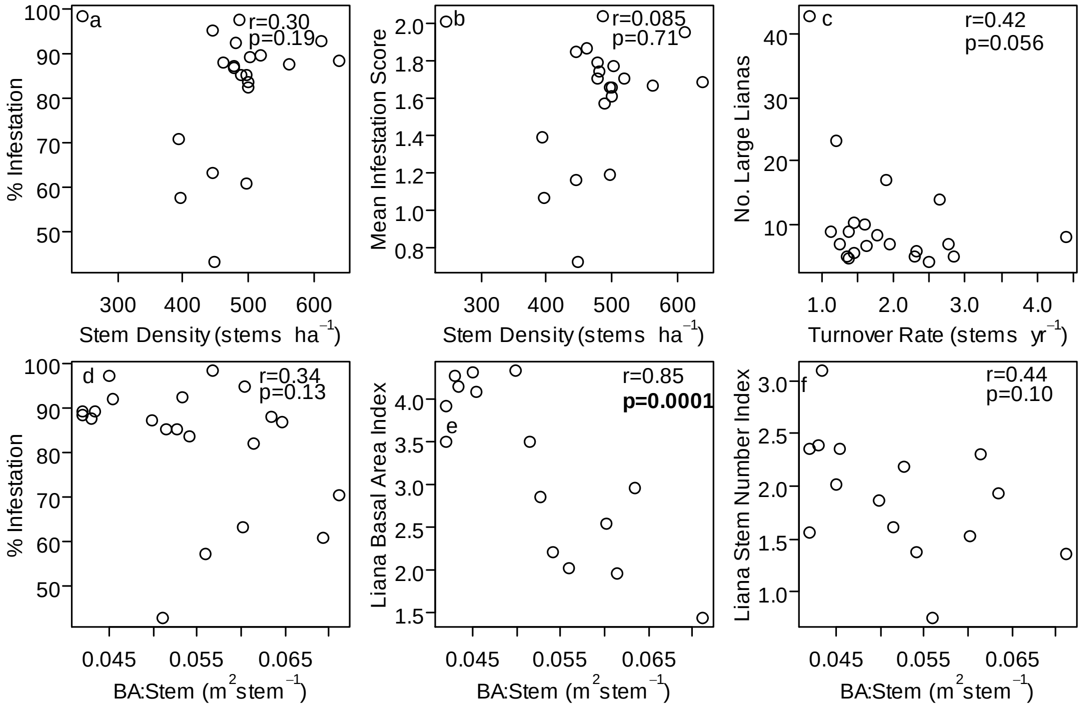

Figure 4.4. Bivariate relationships between liana abundance metrics and spatial variables from the best models of liana distribution. Correlation coefficients and *p*-values are given; significant *p*-values are in bold.

4.4.3 Mixed-effects models of liana spatial distribution

The drivers of liana spatial distribution varied between liana metrics, as shown by the best models chosen by the multi-model selection procedure (Table 4.4), but there is evidence for some clear general patterns. Forest structure variables (stem density and basal area to stem ratio) were the most important predictors of all liana metrics except the number of large lianas (Table 4.4, Fig. 4.4). Liana basal area index and liana stem number index decreased with increasing tree basal area to stem ratio, whilst mean infestation score increased with tree stem density. For the percentage of infested trees both tree stem density and basal area to stem ratio were important. In contrast, the number of large lianas was negatively related to tree turnover rate (Fig. 4.c); turnover had no influence on other liana metrics. Some soil variables were occasionally included in the chosen models, though typically these relationships were individually non-significant; percentage of infested trees, mean infestation score and number of large lianas showed a negative relationship with PC2 (pH axis), and large lianas and liana stem number index decreased with PC1 (fertility axis). Mean annual precipitation was rarely included in the best models and was individually non-significant.

Table 4.4. Estimates of parameters included in the four best mixed-effects models (based on AICc) describing the spatial distribution of each liana metric. All models include forest reserve as a random factor. *p*-values for each parameter estimate are shown as: • < 0.1, * < 0.05, ** < 0.01.

Liana Metric	MAP	PC1	PC2	PC3	Turnover[a]	Stem Density	BA:Stem Ratio	AIC	AICc
% Infested Trees[b]						0.087*		140.2	143.0
			-2.23			0.084*		138.6	143.2
	-0.022·						-596*	140.0	144.6
							-507·	142.1	144.9
Mean Infestation Score			-0.076·			0.003*		9.3	13.9
						0.003*		11.2	14.1
				0.084		0.004*		10.6	15.2
			-0.076·	0.074		0.004*		8.9	15.9
Number ≥ 10 cm[a]		-0.088·			-1.11*			34.6	39.2
					-0.98*			36.6	39.5
	0.0009				-1.09*			36.9	41.5
		-0.093·	-0.083		-1.23*			35.0	42.0
Basal Area Index							-91.8**	29.8	33.8
						0.016**		33.8	37.8
			0.063				-93.7**	31.3	38.0
	0.0005						-87.8**	31.4	38.0
Stem Number Index								31.7	33.9
							-34.4·	30.2	34.2
		-0.091					-44.1*	28.0	34.7
						0.004		31.8	35.8

[a] Log transformed.

[b] Arc sine transformed.

As the results show that forest structure is a key driver of the percentage of trees infested in these plots, it was tested whether changes in forest structure over time may have led to the observed changes in infestation rates between censuses. To do this, relationships between annual rate of change in liana infestation (pp yr^{-1}, where pp is percentage points), annual rate of change in tree stem density (stems ha^{-1} yr^{-1}), and basal area to stem ratio (m^2 $stem^{-1}$ yr^{-1}) were analysed using mixed effects models with forest reserve as a random factor. Tree basal area to stem ratio significantly increased during the study period (t = 3.74, df = 18, $p = 0.002$, two-tailed t-test); there was, however, no significant change over time in tree stem density (t = 0.049, df = 18, $p = 0.96$, two-tailed t-test). Overall, neither change in stem density (F = 0.16, df = 8, $p = 0.70$, Fig. 4.5a) nor change in basal area to stem ratio (F = 1.31, df = 8, $p = 0.29$, Fig. 4.5b) were significantly related to change in infestation rates. However, the negative relationship between change in basal area to stem ratio and change in infestation matches the result from the analysis of liana spatial distribution that the percentage of infested trees is negatively related to basal area to stem ratio.

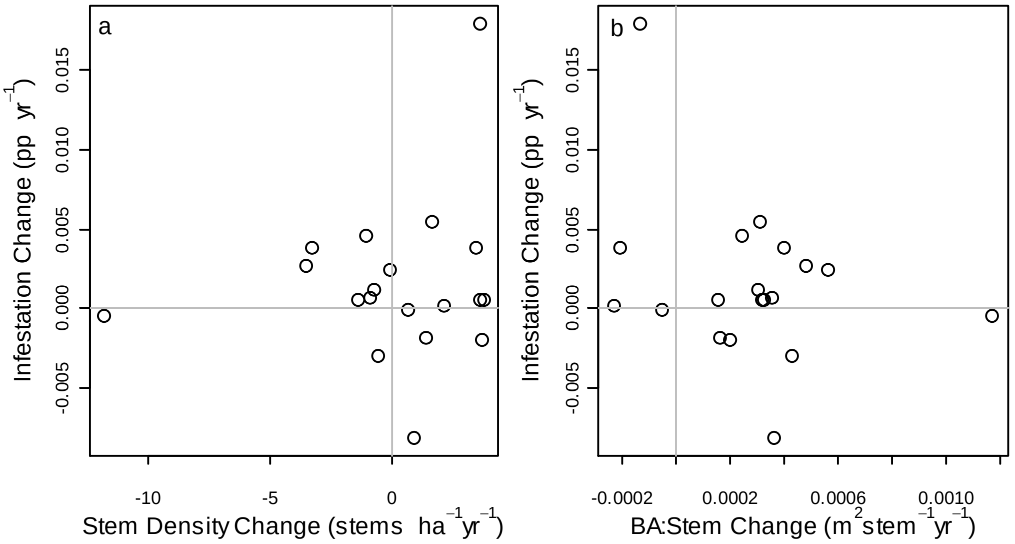

Figure 4.5. Relationships between change in liana infestation over time (percentage points yr^{-1}) and change in forest structure; tree stem density (stems ha^{-1} yr^{-1}) and basal area to stem ratio (m^2 $stem^{-1}$ yr^{-1}).

4.5 Discussion

Liana abundance has increased in Neotropical forests during recent decades but the few data available from Africa does not demonstrate this pattern. These results suggest that the drivers of change in liana abundance are complex and may vary in different landscapes or on different continents. Here, the results from Ghana show a significant but very slight increase over time in the percentage of trees infested with one or more lianas, a proxy for liana abundance. In terms of spatial patterns four of the five liana abundance metrics were strongly linked to variation in forest structure, whilst the abundance of large lianas (≥ 10 cm *Dmax*) was unrelated to forest structure, but increased with lower tree turnover rates. In contrast, climate and soil variables appeared to exert little control over liana abundance. Despite the significant relationships between forest structure and liana distribution, plot-level changes in liana infestation rates were unrelated to changes over time in forest structure.

4.5.1 Drivers of liana spatial distribution

Four of the five metrics of liana abundance (percentage infestation, mean infestation score, liana basal area index and liana stem number index) gave the same overall result that liana abundance increases with higher tree stem density and lower tree basal area to stem ratio. This result of the importance of forest structure for liana distribution is supported by other studies. In eastern Ecuador the number of liana individuals was significantly positively correlated with the abundance of small trees (1 - 10 cm *D*, Nabe-Nielsen 2001) and Laurance *et al.* (2001) found a negative relationship between both liana abundance and liana biomass with tree basal area in Central Amazonia. In addition, across the Neotropics, liana density, but not liana basal area, was significantly but weakly related to tree stem number (van der Heijden & Phillips 2008) and the density of lianas < 5 cm *D* in a Central Amazon forest increased with an increased proportion of small trees (as measured using a vegetation index based on size class distributions, Nogueira *et al.* 2011). This study has shown liana distribution to be linked primarily to forest structure, with most liana metrics increasing in areas with higher tree density and where trees are typically smaller (low basal area to stem ratio). These patterns support the hypothesis that host availability is a key driver of liana distribution as lianas require host trees to reach the canopy and gain access to light (Putz 1984a; Balfour & Bond 1993).

Interestingly, the distribution pattern of large lianas was very different to the other liana metrics. The abundance of large lianas was predominately controlled by tree turnover rate, with higher large liana abundance in plots with lower turnover. This is probably because large lianas require large trees as supports, and presumably require long time-periods to reach such substantial sizes without experiencing host tree mortality. In the Peruvian Amazon, the abundance of large lianas was correlated positively with tree basal area (Phillips *et al.* 2005), which similarly indicates their association with large trees and stable patches of forest with low turnover rates and DeWalt *et al.* (2000) found that along a secondary forest chronosequence large lianas were only found in forests at least 70 years old, whereas small lianas were most common in 20 year old stands. A similar contrast in the relationships between forest structure and lianas of different size classes was found in forests of south west China where lianas ≥ 4 cm *D* showed a strong positive correlation with the abundance of large trees but lianas < 4 cm *D* showed a negative correlation (Yuan *et al.* 2009).

Surprisingly, neither mean annual precipitation (MAP) nor soil fertility (PC1, correlated with MAP) were related to any liana metric. Other studies have shown liana abundance increases with dry season length, and decreases with MAP (Schnitzer 2005; Swaine & Grace 2007; DeWalt *et al.* 2010; Toledo 2011). One reason for the lack of a relationship in this study may be that there was less variation in precipitation regimes within our dataset compared to other studies. It was not possible to assess effectively the impact of dry season length as all forests in this study experienced either 3 or 4 consecutive months with < 100 mm rainfall and the gradient of MAP only varied from 1288 to 1928 mm yr^{-1}. In contrast, the analyses of Schnitzer (2005) and DeWalt *et al.* (2010) are based on datasets including MAP ranges of 500 - 7500 mm yr^{-1} and 860 - 7250 mm yr^{-1} respectively, and the shorter Bolivian rainfall gradient (1110 - 2200 mm yr^{-1}) covers a greater seasonality range of 4 - 7 months (Toledo 2011). Associations between liana abundance and climate may therefore only be visible across larger gradients than included in this study. However, another study carried out in Ghana found liana species richness was negatively related to MAP. The discrepancy between this study and Swaine & Grace (2007) is particularly perplexing as both studies were carried out in the same area. One reason may be that Swaine & Grace (2007) include samples from the driest forests (estimated rainfall minimum 1000 mm) which were not sampled in this study. A second cause of the different results between the studies may be the use of different liana metrics; Swaine & Grace (2007) assess liana species richness as a proportion of all species (lianas, trees and herbs) rather than liana abundance *per se*. As tree species richness declines with increasing rainfall in Ghana (Hall & Swaine 1976) the result may show an increase in the proportion of liana richness even if liana abundance remained constant. Therefore, the result presented by Swaine & Grace (2007) may not reflect an increase in liana abundance in drier sites. Despite the findings of Schnitzer (2005), Swaine & Grace (2007), DeWalt *et al.* (2010) and Toledo (2011), the negative relationship between precipitation and liana distribution has not always been observed. Across 57 Neotropical sites with a MAP range of 400 - 9000 mm yr^{-1} there was only a weak effect of MAP on liana basal area was found and no effect on liana stem density (van der Heijden & Phillips 2008). DeWalt *et al.* (2010) suggest that the small plot area (0.1 ha) used by van der Heijden & Phillips (2008) may not be sufficient to adequately sample variation in liana abundance. However, this is unlikely to be a problem in this study as larger (0.52 - 1 ha) plots were used.

As well as finding no effect of MAP on liana abundance, there was very little association between soils and liana distribution (Table 4). At least along the environmental gradient of the Ghanaian forest zone, the results of this study suggest forest structure is a more important driver of liana distribution than climate or soils. Neither Schnitzer (2005), Swaine & Grace (2007), DeWalt *et al.* (2010) or Toledo (2011) assess the influence of forest structure on liana distribution; further studies including multiple potential drivers of liana abundance are necessary to establish which drivers influence liana distribution at various scales.

4.5.2 Temporal changes in liana abundance

The results show a very slight increase in the percentage of trees infested with lianas from a mean of 78.6 % during the early 1990s to 81.2 % in the late 2000s. This is reflected by the logistic regression analysis showing the probability of a tree carrying a liana increased very slightly over the study period. Our result contrasts with other African studies that have shown 20 % (Caballé & Martin 2001) and 33.5 % (Ewango 2010) localised reductions in liana abundance between 1979 and 1992 and 1994 and 2007 respectively. Studies from the Neotropics show increases in liana abundance; Phillips *et al.* (2002) find an approximate doubling of the number of large lianas in multiple census plots from 1985 to 2002, whilst on Barro Colorado Island the leaf litter dry mass from liana species increased from 0.85 to 1.55 Mg ha^{-1} yr^{-1} from 1986 to 2002 (Wright *et al.* 2004), flower production increased by 4.1 % yr^{-1} between 1987 and 2003 (Wright & Calderon 2006), and the percentage trees ≥ 20 cm *D* infested with lianas increased from 45% in 1980 (Putz 1984a) to 73.6 % in 2007 (Ingwell *et al.* 2010). Increases in large liana abundance and biomass observed in French Guiana were modest, just 4 and 2 additional large lianas in 10 ha and 12 ha plots respectively over 7.5 yr and 9.6 yr intervals, with liana biomass increasing by 0.69 % yr^{-1} and 0.43 % yr^{-1} at the two plots respectively (Chave *et al.* 2008b).

The increase in liana infestation of 0.18 % yr^{-1} found in this study is clearly not as strong as those found in Neotropical studies (Phillips *et al.* 2002; Wright *et al.* 2004; Wright & Calderon 2006; Ingwell *et al.* 2010), but neither does the slight increase follow the results from other African studies (Caballé & Martin 2001; Ewango 2010). Initial liana infestation was very high in the Ghanaian plots (53.1 - 99.0 %, mean 78.6 %, Table 4.3). In comparison, recorded infestation rates for Neotropical forests with 3 - 6 months dry season vary from 49.9 % to 77 % (Carse *et al.* 2000; van der Heijden *et al.* 2008; Ingwell *et al.* 2010) and 57 % of trees were infested in an aseasonal forest in Borneo (Campbell & Newbery 1993). A study from a forest reserve included in this analysis showed a similarly high infestation rate of 88.2 % (Addo-Fordjour *et al.* 2009) and the mean initial liana infestation is only slightly lower than in a Bolivian 'liana forest' where 86.3 % of trees ≥ 10 cm *D* carried a liana ≥ 2 cm *D* (Pérez-Salicrup *et al.* 2001). Individual host tree infestation is known to be linked to host traits (e.g. van der Heijden *et al.* 2008) and it is possible that the majority of trees capable of carrying a liana were already infested at the beginning of the study. This pattern would limit the potential for any further increase to occur. Furthermore, using only infestation data it would not be possible to detect if liana load per infested tree had increased over the study period. Observations of decreases in liana infestation, in contrast, should not be limited by an initially high infestation rate. Overall, the infestation rate of the forest may in fact be a good predictor of the possible changes in liana abundance over time.

If the infestation rates determine potential future changes, it is important to understand why infestation rates vary among forests. The results show that, spatially, liana abundance is strongly determined by forest structure in terms of stem densities and basal area to stem ratio and other studies have shown the importance of tree height (Gerwing & Farias 2000; Parthasarathy 2004). Tree height (Feldpausch *et al.* 2011; Banin *et al.* 2012) and tree diameter class distributions (Feldpausch *et al.* 2012) differ among forests and continents, with trees being on average taller and wider but with lower stem densities in African compared to Neotropical forests. This variation in forest structure may cause variation in liana populations in addition to the effects of climate and soil. In turn, this broad variation in liana infestation rates may strongly affect the observed temporal trends.

Two changes in Ghanaian forests during the past decades may also have influenced liana abundance in the region. Firstly, over the past twenty years forest structure has changed: basal area has increased whilst stem numbers remained constant. This has resulted in increased basal area to stem ratios which, as shown by our analysis of the drivers of liana spatial distribution, may be expected to decrease liana abundance. Secondly, Ghanaian forests have experienced an 11 % decrease in MAP since the early 1970s (Chapter 2) which may be expected to increase liana abundance according to the hypothesis of Schnitzer (2005). At the plot level, there is only a weak relationship between change in basal area to stem ratio and change in liana infestation, and no relationship between change in stem density and change in liana infestation. This suggests altered forest structure has not driven changes over time in liana infestation. However, the increase in water stress may have counteracted the potentially negative effect of increased basal area to stem ratio on liana abundance.

Understanding drivers of temporal change in liana abundance remains a challenge, even with knowledge of the local drivers of liana spatial distribution. However, separating out and analysing liana size classes independently may help to understand some of these patterns. Although large lianas ≥ 10 cm contribute large proportions of basal area and biomass to the overall liana community (Phillips *et al.* 2005), in terms of stem density the contribution is small (Putz 1984a; Hegarty & Caballé 1991). Using the liana survey data collected in this study, only 0.4 % of liana stems reached 10 cm diameter, comparable to the findings of Laurance *et al.* (2001) who found only 2.9 % were above this threshold, and Reddy & Parthasarathy (2003) who found only 18 % of lianas were ≥ 6 cm. This study and others show that large lianas display different relationships with biotic and abiotic variables compared to the liana community as a whole (DeWalt *et al.* 2000; Laurance *et al.* 2001; Yuan *et al.* 2009; Nogueira *et al.* 2011); in this study large liana abundance was negatively correlated to forest turnover rate, whilst all other metrics showed liana abundance was related to forest structure (Table 4). Therefore, analysing changes over time of lianas in different size classes may help to disentangle to roles of different drivers.

Schnitzer & Bongers (2011) discuss four hypothesised drivers of increasing liana abundance: increased evapotranspiration, increasing rates of natural disturbance, changing land-use and elevated atmospheric CO_2. Of these potential drivers, increased rates of natural disturbance and changing land-use are likely to increase the abundance of smaller lianas whilst having a negative impact on the abundance of large lianas. In contrast, the other hypotheses, increased evapotranspiration and elevated atmospheric CO_2, would likely affect all liana size classes. An additional hypothesis may be that changes in forest structure have affected liana abundance. For example, increased basal area may promote large liana abundance and an increase in stem density may increase the abundance of lianas of smaller size classes. However, few studies explicitly examine trends in different size classes: the observed increases in liana abundance across the Amazon are based only on large lianas (Phillips *et al.* 2002), whereas the increases on Barro Colorado Island are more likely representative of the liana community as a whole

(Wright *et al.* 2004; Wright & Calderon 2006; Ingwell *et al.* 2010). Hence, it is quite possible that different mechanisms may be responsible for the increases in the different studies. This study shows the importance of considering liana size class in assessing both spatial and temporal patterns of liana abundance.

In conclusion, of the variables included in our analysis, the majority of liana metrics were related to forest structure, whilst the distribution of large lianas was related to forest turnover rates. Evidence for a pantropical temporal trend in liana abundance remains unclear given the contradictory evidence from the few studies from Africa, including the marginal increase found by this study in Ghanaian forests, and the absence of studies from Asia. Overall, these results confirm that recent changes in liana abundance are landscape-specific, and that we should not expect a simple global driver or trend.

5. Conclusions

5.1 Overview of findings

This thesis aims to make use of a long-term dataset from across the forest zone of Ghana to assess key questions regarding threats to tropical forests. The main objectives were 1) to assess the impacts of long-term drought on forest functional composition and structure, 2) to test if past fires have a long-term impact on forest structure and composition, and 3) to test if lianas have increased over recent decades in Ghanaian forests, and the drivers of their spatial distribution.

The studies contained within this thesis have produced three main original findings. First, I show for the first time that long-term drought can impact forest composition across a variety of forest types, causing a shift towards more drought-tolerant species. Furthermore, I demonstrate that despite this impact on species composition, drought does not necessarily lead to biomass loss as has been shown in other short-term studies. This suggests that shifting species composition in favour of drought-tolerant species increases the resilience of tropical forests to long-term drought. Second, I present the longest study of post-fire regeneration from tropical forests. This study shows that, even after 15 - 27 years since the fires, burnt forests which experienced high fire intensity are still significantly altered in structure and functional and species composition. However, forest structure shows clear signs of recovery over this time period, with some plots reaching stem density and biomass values of unburnt plots. Third, in contrast to the large increase in lianas observed in the Neotropics, I find only a very slight increase in the percentage of infested trees over the two decade study period. Furthermore, I find no support for the hypothesis that liana spatial distribution is driven by water stress; rather, forest structure is the main driver. Importantly, large lianas (≥ 10 cm maximum diameter) showed different spatial patterns to the liana community as a whole as forest turnover was the strongest predictor of large liana distribution.

Overall, these results show that, for Ghanaian forests and the threats assessed in this thesis, the impact of fire has the largest and most lasting impact on forest structure and composition. This is because forests appear resilient to the long-term drought that has occurred since the early 1970s, and the infestation rates of trees by lianas has remained relatively constant. However, even with decades in which to recover, some burnt forests still contain lower biomass and basal area and an altered species composition.

5.1.1 Long-term drought in Ghanaian forests

Comparing patterns of change in functional traits observed in Ghanaian forests to hypothesised changes due to drought, past disturbance, current disturbance and nutrient enrichment, the impact of drought was most strongly supported by the results: drought-tolerant and deciduous species increased over the study period. I tested this further by assessing the relationship between functional trait composition and mean annual precipitation along the rainfall gradient. The majority of traits that increased or decreased significantly over time also increased or decreased along the rainfall gradient, confirming that the overall changes found, including such shifts as an increase in canopy species and decreases in sub-canopy and shade-tolerant species, were supported by the spatial patterns in trait composition. Furthermore, traits that did not show significant changes over time, such as wood density and understorey trees, also showed no relationship with the precipitation gradient. However, above ground biomass and basal area, which increased over time, did not change along the precipitation gradient, suggesting altered precipitation regimes have not led to the observed shifts in forest structure. Other studies assessing the impact of more intense droughts show increased mortality and biomass loss (van Nieuwstadt & Sheil 2005; Phillips *et al.* 2009a; da Costa *et al.* 2010). I hypothesise that the long-term but relatively weak drought experienced in Ghanaian forests has caused a shift in species composition to favour species better adapted to greater water stress. As the long-term history of Ghanaian forests includes an approximately 40 year wet - dry cycle the drought experienced since 1970 is not necessarily anomalous, and the species pool is likely adapted to such changes. This shift in species composition to species more tolerant of water stress may have enabled forest structure to be maintained during this period. However, as the study period for the plot network (mean census dates 1991.84 - 2008.91) did not date back to the pre-drought period I cannot exclude the possibility that initially the drought may have lead to biomass loss, and since then the biomass store has been recovering. The lack of increase in shade-tolerant species and lack of change in plot-level mean wood density, however, do not show such signs of recovery from past disturbance. Furthermore, the shift in habitat score in the 40 year dataset from the Kade plots dates back to the onset of the drought suggesting this increase in drought-tolerance has been consistent since then.

5.1.2 Long-term impacts of fire in Ghanaian forests

Past fire events had a significant impact on both forest structure and functional composition, even when measured 15 - 27 years after the most recent fire event. Fire intensity, as measured by assessing fire scars on surviving trees, was a good predictor of the difference in structural and compositional variables between plots. Using the dataset of 10 plots, three unburnt, three once burnt and four twice burnt plots, there were clear relationships between fire intensity and stem density and above ground biomass. The most heavily burnt plots had the lowest biomass and stem densities. However, burnt plots also showed high stem recruitment and biomass growth rates. Except for one plot which decreased in biomass, all burnt plots increased in both stem density and biomass over the study period, showing evidence of recovery since the fire events. Compared to the estimated 1983 unburnt plot means, two burnt plots approached or surpassed the equivalent stem density, and three plots the equivalent biomass, of unburnt plots. Based on extrapolations of the growth, recruitment and mortality of the burnt plots, I estimate that it would take up to 70 years for all burnt plots to recover stems and biomass to the equivalent of unburnt plots, however some plots may do so as soon as 20 years after fire.

Functional composition also showed significant impacts of fire intensity. More intensely burnt plots contained a higher percentage of low wood density, pioneer species. These species also showed high recruitment over the study period, showing there was little evidence of a shift away from a composition characteristic of disturbed forest. With increasing fire intensity, plots contained fewer understorey species and had higher plot mean bark thickness. These differences are likely due to fire-induced mortality rather than recruitment of early successional species as small understorey tree with thin bark are more likely to be killed by fire. Interestingly, the data also shows that thicker-barked species recruited into burnt plots following fire events, possibly because parent trees of thicker-barked species are more abundant in burnt forest. The lack of evidence of recovery of functional composition similar to unburnt plots suggests that the recovery of composition will take longer than the recovery of forest structure. The results presented here support those of other studies proposing that structure can recover in shorter time-periods than composition (Slik *et al.* 2002; Barlow & Peres 2008), but provides a substantially longer post-fire recovery period than these previous studies.

5.1.3 Temporal changes and spatial trends in liana abundance

I find that liana infestation increased very slightly but significantly over the two decade study period, in contrast to other studies from African forests reporting decreases in liana abundance (Caballé & Martin 2001), and widespread increases in liana abundance in the Neotropics (Phillips *et al.* 2002; Wright *et al.* 2004; Ingwell *et al.* 2010). Spatially, four out of five liana abundance metrics were driven by forest structure, increasing with stem density and decreasing with basal area to stem ratio. In contrast, the abundance of large lianas was negatively related to stem turnover. This is important as the evidence of liana increase from a widespread plot network is derived only from large lianas (Phillips *et al.* 2002), and my results suggest that drivers of large liana abundance may be different to the drivers of the liana community as a whole. Furthermore, a hypothesised driver of liana spatial distribution and recent increases in the Neotropics is related to water stress, with liana abundance hypothesised to increase with water stress. However, along the precipitation gradient in Ghana (c. 1200 - 2000 mm yr^{-1}) I do not find any effect of precipitation on liana abundance, although it is possible that such patterns are only apparent over wider rainfall gradients, or that seasonality of rainfall is more important than total rainfall. A further result of interest from the study is the importance of forest structure in determining liana spatial distributions which may have relevance for the different temporal patterns in Africa and the Neotropics. Evidence is developing for differences in forest structure between the different tropical continents. For example, trees reach taller maximum heights in Asia and shorter maximum heights in Amazonia, with African forests intermediate (Feldpausch *et al.* 2011; Banin *et al.* 2012). Furthermore, stem density varies between forest regions, with African forests typically holding fewer stems than Amazon forests, but with African forests containing higher basal area and biomass (S.L. Lewis, pers. comm.). Stem turnover rates are also low in Africa, more typical of low turnover Eastern Amazonian forests than the higher turnover Western Amazonian forests (S.L. Lewis, pers. comm.). As liana distribution is related to forest structure and dynamics, these differences between continents may contribute to the differences found in recent changes in liana abundance in Africa and the Neotropics.

5.2 Research Implications

5.2.1 Implications for Ghanaian forests

Of the potential threats to forests assessed in this thesis, drought, fire and liana infestation, I find that fire is the strongest threat. Using the Walker *et al.* (2004) definition of resilience as “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks”, Ghanaian forests appear largely resilient to the multi-decade drought experienced since the 1970s. This resilience to long-term drought is likely due to the long history of wet – dry cycles experienced over millennia in West African forests (Shanahan *et al.* 2009) and extensive human presence in the area leading to a high number of drought- and disturbance-tolerant taxa in the regional species pool. Future droughts of similar magnitude interspersed with wetter periods are likely to occur in Ghana, following past trends in climate (Shanahan *et al.* 2009). Such conditions are unlikely to result in detrimental effects on Ghanaian forests. Resilience to more severe droughts, however, may not be so high. Furthermore, the diverse nature of the forests studied was clearly important, and degraded forests with limited species diversity may not necessarily show such resilience. Liana infestation is known to increase tree mortality and reduce tree growth rates (Clark & Clark 1990; Phillips *et al.* 2005; van der Heijden & Phillips 2009a; Ingwell *et al.* 2010). Therefore any increase in liana infestation would have a detrimental impact on tropical forest trees. In Ghana liana infestation rates were already high at the beginning of the census interval, and over the twenty year study period I find very little change in liana infestation rates, suggesting that forest dynamics are unlikely to be affected by shifts in liana abundance. As infestation rates of trees were high throughout, this may suggest a long history of infestation to which the tree species have already adapted.

In contrast to drought and liana infestation, the occurrence of forest fires is of considerable concern for Ghanaian forests. Functional composition remained significantly altered in burnt forests compared to unburnt controls, even after 15 – 27 years of regeneration since fire. Forest structure showed recovery in all plots, with those experiencing the lowest fire intensities approaching or surpassing stem desnity and biomass of unburnt plots, however the forest sturtcures of areas with the highest fire intensities were still strongly affected. At broader scales, these impacts may be an underestimate. In this thesis only forests within the moist semi-deciduous forest type were included; the dry semi-deciduous forest zone has been even more severely impacted by fire since the strong ENSO event in 1982/83 (FORIG 2003). In this region, repeated burning has occurred in some areas resulting in degradation of forest reserves and invasion by exotic species such as the weedy vine *Chromolaena odorata*, the invasive tree species *Broussonetia papyrifera,* and *Panicum maximum* grass (Swaine *et al.* 1997). Presence of *C. odorata* was noted in open areas in some heavily burnt plots during data collection, as well as in areas opened by logging activities such as old hauling roads. Furthermore, heavily burnt and logged plots within Tinte Bepo forest reserve which could not be included in analysis contained a high density of *B. papyrifera* trees. The presence of these invasive species will likely limit the regenerative capacity of native species in degraded areas. This is of economic significance for Ghana as selective logging for timber is a major source of revenue.

The wildfires in 1983 had a considerable impact in Ghana and alerted the Ghanaian government to the problem. Across the country the fires destroyed an estimated 35 % of crops and stored cereals (Ampadu-Agyei 1998) and the revenue loss from the destruction of timber has been valued at $24 million (FORIG 2003). After the 1983 fires new laws were implemented with an emphasis on punishing those who ignite fires, but the law did not have much impact (Kalame *et al.* 2009). Improvements were made with 2006 National Wildfire Management Policy with a more holistic approach including stakeholder participation in fire management (MLFM 2006; Kalame *et al.* 2009). The activities of farmers using fire for land management altered after the 1983 fires with more people constructing fire belts and using the services of fire volunteers (Amissah *et al.* 2010). If successfully implemented, the response of both the government and farmers to the fire outbreaks should decrease the occurrence of wild fires which may spread into forested areas. The long-term impacts of fires on forest structure and composition found in this thesis emphasise the importance of fire prevention activities.

These activities do not, however, tackle the issue of forest flammability. In order to focus on the key issues of drought, fire and lianas, logged areas were excluded from analysis. However, logging and other forms of anthropogenic forest degradation are a significant issue for Ghanaian forests (Agyarko 2001; Alo & Pontius 2008), and in particular influence the flammability of the forest. The remaining old growth forest occurs within designated forest reserves and a smaller number of national parks. Areas outside of the protected areas have been mostly deforested. Tree felling within national parks is illegal, but within forest reserves concessions are sold to timber companies to extract a limited quantity of trees. In addition to these legal activities, further pressure comes from illegal tree felling and other disturbances such as gold mining and farming (Agyarko 2001). As described at the beginning of this thesis (Section 1.3.2) forest degradation increases forest flammability. The remaining forests are already highly fragmented which again increases flammability. Furthermore, previously burnt forest areas have also been affected by salvage logging, where the last remaining commercial trees are removed before conversion to other land uses such as agriculture or plantations. These activities are likely to again increase flammability and the spread of fires into previously unaffected areas. Increased temperatures and increased drought occurrence due to climate change may also increase forest flammability. The interactions between socio-economic drivers of land use and climate may exacerbate fire risk. Even with the possibility of reduced ignition sources due to government policy, the risk of fires in Ghanaian forests may remain high, especially in years of low rainfall; a continued commitment to fire reduction will be essential for the future of Ghanaian forests.

Fig. 5.1 shows the conceptual model of threats to tropical forests and the impacts of these threats originally presented in Section 1.1 adapted to reflect the processes highlighted in this thesis. The importance of fire for species composition change, tree mortality, change to forest structure and the presence of invasive species are emphasised in Fig. 5.1, as well as the causes of fire occurance and the influence of drought on species composition. The link between climatic drivers of increased liana infestation have been removed, as only a very slight increase in infestation was found during the study period which included a long-term drought, and the potential impacts of increased liana infestation have also been removed as other processes are of greater significance for Ghanaian forests. However, links between forest structure and tree mortality (related to turnover) and liana abundance have been added as the spatial distribution of lianas was found to be related to these factors.

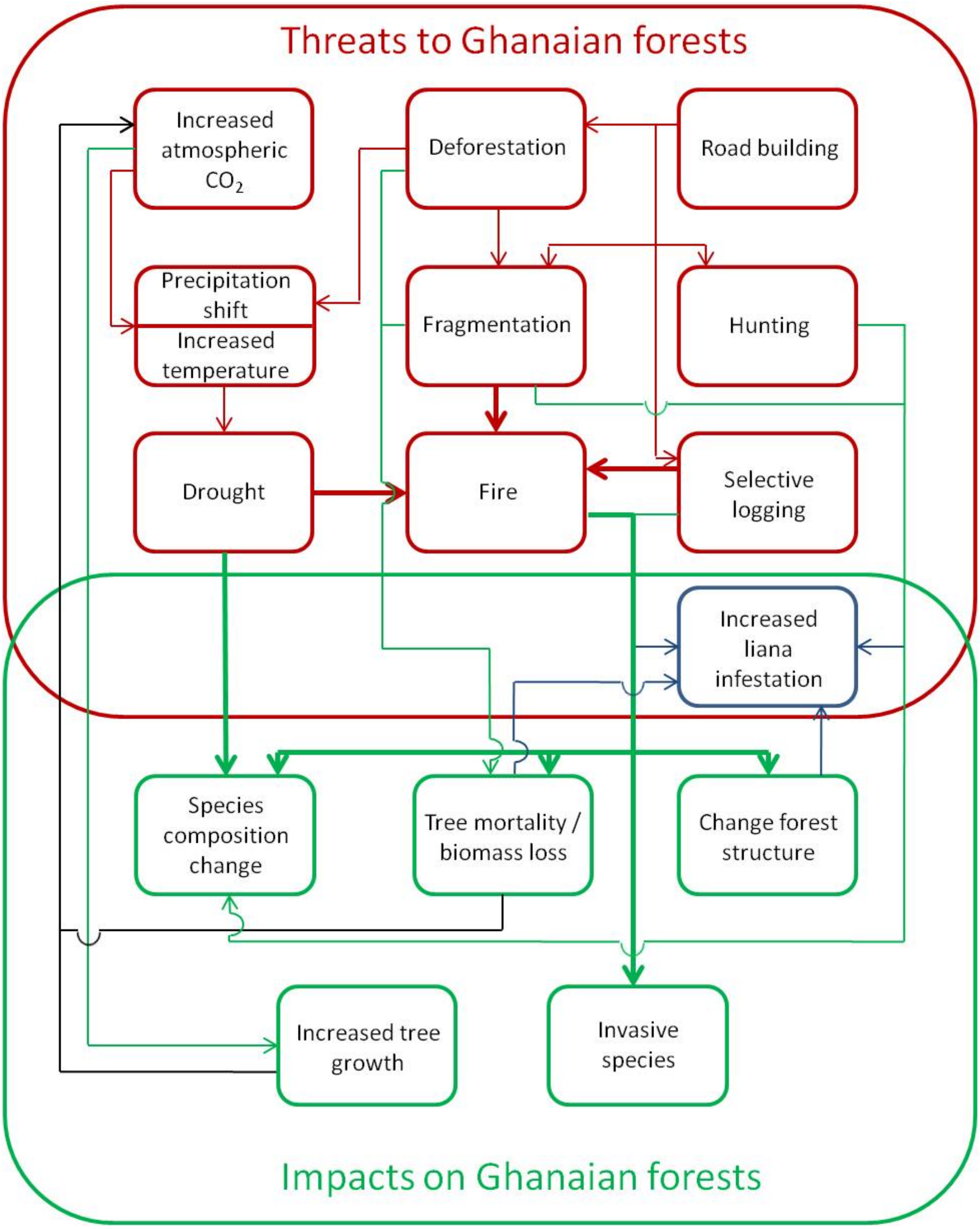

Figure 5.1. Conceptual model of threats to Ghanaian forests and their impacts, informed by the studies included in this thesis. Threats are shown in red, with red arrows representing interactions between threats, impacts of threats are shown in green, increased liana abundance which could be considered both a threat and an impact is shown in blue and the feedbacks of tree mortality and tree growth to atmospheric CO_2 concetration is shown in black. Bold lines show the processes found to be particularly important for Ghanaian forests.

5.2.2 Implications for the tropical forest biome

The results of this thesis have implications not only for Ghana, but for the whole tropical forest biome.

A key result is the long timescale of recovery from forest fires. This result is supported by other studies assessing shorter post-fire periods (Slik *et al.* 2002; Barlow & Peres 2008). Depending on the extent of initial fire damage, it may take up to 70 years for stem densities and aboveground biomass to recover to pre-disturbance levels, and even longer to develop a composition similar to unburnt forests. Increased fire occurrence is predicted for many tropical regions due to the combination of land use change, direct anthropogenic disturbance and climate change (e.g. Soares-Filho *et al.* 2012). Given the large areas already burnt and that may be burnt in the future, and the time required for full recovery, it is likely that in the future vast areas of forest will be at some stage of regeneration from fire. These issues are important for the climate change mitigation strategy REDD+ (Reduced Emissions from Deforestation and Degradation) which is based on payments for avoiding carbon emissions from deforestation and forest degradation (Laurance 2007). If forests under a REDD+ scheme burn, a significant amount of carbon would be emitted and a decadal scale time-period would be required to recover the emitted carbon. As proposed by Aragão & Shimabukuro (2010) fire prevention activities should be included in REDD+ projects to ensure continued carbon storage, and the risk of fire should be included in the design of these initiatives (Baker *et al.* 2010).

Scaling up the results of the drought study to other areas is more complex. The tree taxa in Ghana may have already experienced a selective filter of climatic and anthropogenic disturbance resulting in a pool of species resistant to some environmental changes. As such, areas that have experienced more constant climates and forest cover over geological time scales, for example Amazonia (Anhuf *et al.* 2006) may not respond to weak but long-term droughts in the same way. Other African forests with similar long-term history are more likely to show similar patterns. This is good news for West and

Central African forests if climate change leads to increased water stress of a similar magnitude to that analysed in this study. The fact that shifts in species composition and increases in biomass were found across a variety of forest types also suggests this effect may be exhibited by other African forests, including wetter areas. I hypothesise that the presence of species rich flora representing a range of life-history strategies is important for the maintenance of forest under water stress. Therefore, for forests to have the maximum capacity to survive climate change the full suite of species must be present. This again has relevance for REDD+, emphasising the importance of biodiversity conservation for the maintenance of forest carbon stocks (Grainger *et al.* 2009).

The findings presented here concerning trends in liana infestation support other evidence that African forests are not exhibiting the same large increases in liana abundance that have been shown in Neotropical forests. This pattern has two possible consequences for the discussion on the drivers of increased liana abundance: either the driver(s) of increased liana abundance is not acting globally, or differences between the continents are preventing a global driver(s) from resulting in increased liana abundance in Africa. A final key result is that liana distribution is most strongly driven by forest structure and dynamics, suggesting liana abundance may also alter if forest structure and dynamics change.

5.3 Future research directions

The results from this thesis provide many avenues of future research. Firstly, I show tropical forests can be surprisingly resilient to long-term drought. However, the generality of this result is unclear and it would be fascinating to test this at a broader scale, assessing composition and biomass change in forest locations experiencing different shifts in climate. Continuing to monitor the plot network in Ghana in the coming years could provide further insight into the impact of climate on forest composition, especially if, as would be expected from the cyclic precipitation history, rainfall increases in the next decade.

The fire study provides a second avenue for future research. Fire intensity was a significant predictor of many structural and compositional variables, adding to the body of evidence showing its importance to the impact of fire on forests. Remote sensing of fires is still limited to hot pixel occurrence (typically including only deforestation fires) and mapping burnt areas of understorey fires. To truly capture the impact of fire it is important to include some measure of intensity or impact, such as reduction of stem density or increase in canopy openness. Development of improved remote sensing to include such measures and linking them to estimated losses of biomass would improve quantification of emissions resulting from fires. In addition, I found evidence of regeneration of forest structure after forest fires, and impacts of fires on forest dynamics. To fully quantify emissions from forests it is also necessary to incorporate such regrowth; vegetation models could be developed to achieve this.

Finally, the assessment of the drivers of liana spatial distribution raises a multitude of further questions. Contrary to some studies, climate did not correlate with liana abundance. It is possible that this is due either to the relative homogeneity of seasonality among the study plots or to the relatively short rainfall gradient in comparison larger scale studies. In order to fully test the influence of climate, forest structure, disturbance and soil fertility, a global scale study is needed including data on all drivers. To date, studies assessing all potential drivers have only been carried out within a single region. An understanding of the drivers of liana abundance, and the scales at which drivers operate, is important to inform the discussion of drivers of increased liana abundance in the Neotropics. I have shown the importance of different liana size classes for assessing the roles of drivers of liana spatial distribution; further studies could investigate shifts in the abundance of small lianas in the Amazon where increases in large lianas have been found.

5.4 Summary

Forest fires with high fire intensity were found to have a large and long-lasting impact on tropical forest structure and composition, more so than long-term drought, whilst increased tree mortality and decreased tree growth due to increased liana abundance does not appear to be a threat to Ghanaian forests. These results are relevant to tropical forest management and policy; the prevention of fire occurrence should be a priority in tropical forest regions, as should the maintenance of biodiversity to maximise the resilience of forest to external changes.

References

Addo-Fordjour, P., Obeng, A., Addo, M.G. & Akyeampong, S. (2009). Effects of human disturbances and plant invasion on liana community structure and relationship with trees in the Tinte Bepo forest reserve, Ghana. *Forest Ecol. Manag.*, 258:728-734.

Addo-Fordjour, P. Rahmad, Z.B & Shahrul, A.M.S. (*in press*). Effects of human disturbance on liana community diversity and structure in a tropical rainforest, Malaysia: implications for conservation. *J. Plant Ecol.*, doi: 10.1093/jpe/rts012

Affum-Baffoe, K. (1996). Revised permanent sample plot procedures in Ghana. In: *IUFRO conference on growth studies in moist tropical forests in Africa*, (eds. Foli, E.G., Vanclay, J.K. & Ofosu-Asiedu, A.). Forestry Research Institute of Ghana, Kumasi, pp. 35-42.

Agyarko, T. (2001). FAO Forestry Outlook Study for Africa (FOSA) Ghana. FAO, Rome.

Alder, D. & Synnott, T.J. (1992). *Permanent sample plot techniques for mixed tropical forests*. Oxford Forestry Institute, Oxford.

Alencar, A., Asner, G.P., Knapp, D. & Zarin, D. (2011). Temporal variability of forest fires in eastern Amazonia. *Ecol. Appl.*, 21, 2397-2412.

Alencar, A., Nepstad, D. & Vera-Diaz, M.D.C. (2006). Forest understory fire in the Brazilian Amazon in ENSO and Non-ENSO years: Area burned and committed emissions. *Earth Interact.*, 10, 1-16.

Alencar, A.A.C., Solórzano, L.A. & Nepstad, D.C. (2004). Modeling forest understory fires in an eastern Amazonian landscape. *Ecol. Appl.*, 14, S139-S149.

Alo, C.A. & Pontius Jr., R.G. (2008). Identifying systematic land-cover transitions using remote sensing and GIS: the fate of forests inside and outside protected areas of Southwestern Ghana. *Environ. Plann. B.*, 35, 280-295.

Amissah, L., Kyereh, B. & Agyeman, V.K. (2010). Wildfire incidence and management in the forest transition zone of Ghana: farmers' perspectives. *Ghana. J. For.*, 26, 61-73.

Ampadu-Agyei, O. (1998). Bushfires and management policies in Ghana. *Environmentalist*, 8, 221-228.

Andrade, J.L., Meinzer, F.C., Goldstein, G. & Schinitzer, S.A. (2005). Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees*, 19, 282-289.

Anhuf, D., Ledru, M.-P., Behling, H., Da Cruz Jr., F.W., Cordeiro, R.C., Van der Hammen, T., Karmann, I., Marengo, J.A., De Oliveira, P.E., Pessenda, L., Siffedine, A., Albuquerque, A.L. & Da Silvas Dias, P.L. (2006). Paleo-environmental change in Amazonian and African rainforest during the LGM. *Palaeogeogr. Palaeocl.*, 239, 510-527.

Aragão, L.E.O.C., Malhi, Y., Roman-Cuesta, R.M., Saatchi, S., Anderson, L.O. & Shimabukuro, Y.E. (2007). Spatial patterns and fire response of recent Amazonian droughts. *Geophys. Res. Let.*, 34, 1-5.

Aragão, L.E.O.C. & Shimabukuro, Y.E. (2010). The incidence of fire in Amazonian forests with implications for REDD. *Science*, 328, 1275 - 1278.

Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R. & Emerson, R. (2009). A contemporary assessment of change in humid tropical forests. *Conserv. Biol.*, 23, 1386-1395.

Avissar, R., da Silva, R. R. & Werth, D. (2006). Impacts of tropical deforestation on regional and global hydroclimatology. In Laurance, W.F. & Peres, C.A. (Eds.) *Emerging threats to tropical forests*. The University of Chicago Press, Chicago.

Baker, T.R., Jones, J.P.G., Rendón Thompson, O.R., Román Cuesta, R.M., del Castilla, D., Chan Aguilar, I., Torres, J. & Healey, J.R. (2010). How can ecologists help realise the potential of payments for carbon in tropical forests countries? *J. Appl. Ecol.*, 47, 1159-165.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Silva, J.N.M. & Martínez R.V. (2004a). Increasing biomass in Amazonian forest plots. *Philos. T. Roy. Soc. B.*, 359, 353-365.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, J.N.M. & Martínez R.V. (2004b). Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob. Change Biol.*, 10, 545-562.

Balch, J.K., Nepstad, D.C., Brando, P.M., Curran, L.M., Portela, O., de Carvalho Jr., O. & Lefebvre, P. (2008). Negative fire feedback in a transitional forest of southeastern Amazonia. *Glob. Change. Biol.* 14, 1-12.

Balch, J.K., Nepstad, D.C., Curran, L.M., Brando, P.M., Portela, O., Guilherme, P., Reuning-Scherer & de Carvalho Jr., O. (2011). Size, species, and fire behaviour predict tree and liana mortality from experimental burns in the Brazilian Amazon. *Forest Ecol. Manag.*, 261, 68-77.

Balfour, D.A. & Bond, W.J. (1993). Factors limiting climber distribution and abundance in a southern African forest. *J. Ecol.*, 8, 93-100.

Banin, L., Feldpausch, T.R., Phillips, O.L., Baker, T.R., Lloyd, J., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bradford, M., Brienen, R., Davies, S., Drescher, M., Higuchi, N., Hilbert, D., Hladik, A., Iida, Y., Abu Silam, K., Kassim, A.R., King. D.A., López-González, G., Metcalfe, D., Nilus, R., Peh, K.S.-H., Reitsma, J.M., Sonké, B., Taedoumg, H., Tan, S., White, L., Wöll, H. & Lewis, S.L. (2012). What controls forest architecture? Testing environmental, structural and floristic drivers. *Glob. Ecol. Biogeogr.* DOI: 10.1111/j.1466-8238.2012.00778.x

Barker, M.G. & Pérez-Salicrup. D. (2000). Comparative water relations of mature mahogany (*Swietenia macrophylla*) trees with and without lianas in a subhumid, seasonally dry forest in Bolivia. *Tree Physiol.*, 20, 1167-1174.

Barlow, J., Lagan, B.O. & Peres, C.A. (2003a). Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *J. Trop. Ecol.*, 19, 291-299.

Barlow, J. & Peres, C.A. (2004). Ecological responses to El Niño-induced surface fires in central Brazilian Amazonia: management implications for flammable tropical forests. *Phil. Trans. R. Soc. B.* 359, 367-380.

Barlow, J. & Peres, C.A. (2006). Consequences of cryptic and recurring fire disturbances for ecosystem structure and biodiversity in Amazonian forests. In Laurance, W.F. & Peres, C.A. (Eds.) *Emerging threats to tropical forests.* The University of Chicago Press, Chicago.

Barlow, J. & Peres, C.A. (2008). Fire-mediated dieback and compositional cascade in an Amazonian forest. *Phil. Trans. R. Soc. B.*, 363, 1787-1794.

Barlow, J., Peres, C.A., Lagan, B.O. & Haugaasen, T. (2003b). Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.*, 6, 6-8.

Barlow, J., Silveira, J.M. & Cochrane, M.A. (2010). Fire scars on Amazonian trees: Exploring the cryptic fire history of the Ilha de Maracá. *Biotropica*, 42, 405-409.

Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L. & Shabel, A.B. (2004). Assessing the causes of late Pleistocene extinctions on the continents. *Science*, 306, 70-75.

Bartoń, K. (2012). MuMIn: Multi-model inference. R package version 1.7.2. http://CRAN.R-project.org/package=MuMIn

Benítez-Malvido, J. & Lemus-Albor, A. (2006). Emerging infectious-disease threats to tropical forest ecosystems. In Laurance, W.F. & Peres, C.A. (Eds.) *Emerging threats to tropical forests*. The University of Chicago Press, Chicago.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.*, 24, 127-135.

Bongers, F., Poorter, L., Hawthorne, W.D. & Sheil, D. (2009). The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to diversity. *Ecol. Lett.*, 12, 798-805.

Bongers, F., Poorter, L., Van Rompaey, R.S.A.R. & Parren, M.P.E. (1999). Distribution of twelve moist forest canopy tree species in Liberia and Côte D'Ivoire: Response curves to a climatic gradient. *J. Veg. Sci.*, 10, 371-382.

Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. & Putz, F.E. (2012). Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behaviour. *Global Change Biol.*, 18, 630-641.

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. *Phil. Trans. R. Soc. B.*, 363, 1839-1848.

Burnham, K.P. & Anderson, D.R. (2004). Multimodel inference: Understanding AIC and BIC in Model Selection. *Sociol. Method. Res.*, 22, 241-304.

Bush, M.B., Silman, M.R. & Listopad, C.M.C.S. (2007). A regional study of Holocene climate change and human occupation in Peruvian Amazon. *J. Biogeogr.*, 34, 1342-1356.

Caballé, G. & Martin, A. (2001). Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecol.*, 152, 167-173.

Cai, Z.-Q., Schnitzer, S.A. & Bongers, F. (2009). Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia*, 161, 25-33.

Caldwell, M.M., Dawson, T.E. & Richards J.H. (1998). Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, 113, 151-161.

Campbell, E.L.F. & Newbery, D.M. (1993). Ecological relationships between lianas and trees in a lowland rain forest in Sabah, East Malaysia. J. Trop. Ecol., 9, 469-490.

Carlquist, S. (1991). Anatomy of vine and liana stems: a review and sysnthesis. In: *The Biology of Vines* (Eds. Putz, F.E. & Mooney, H.A.). Cambridge University Press, Cambridge.

Carse, L.E., Fredericksen, T.S. & Licona, J.C. (2000). Liana-tree species associations in a Bolivian dry forest. *Trop. Ecol.*, 41, 1-10.

Carsten, L.D., Juola, F.A., Male, T.D. & Cherry, S. (2002). Host associations of lianas in a south-east Queensland rain forest. *J. Trop. Ecol.*, 18, 107-120.

Chave, J., Andalo, C., Brown. S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B. & Yamakura, T. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145, 87-99.

Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S., Co. L.L., Dattaraja, H.S., Davies, S.J., Esufali, S., Ewago, C.E.N., Feeley, K.J., Foster, R.B., Gunatilleke, N., Guntailleke, S., Hall., P., Hart, T., Hernández, C., Hubbell, S.P., Itoh, A., Kiratiprayoon, S., LaFrankie, J.V., Loo de Lao, S., Makana, J.-R., Noor, N.S., Kassim, A.R., Samper, C., Sukumar, R., Suresh, H.S., Tan, S., Thompson, J., Tongco, D.C., Valencia, R., Vallejo, M., Villa, G., Yamakura, T., Zimmerman, J.K. & Losos, E.C. (2008a). Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology*, 6, 455-462.

Chave, J., Olivier, J., Bongers, F., Châtelet, P., Forget, P-M., van der Meer, P., Norden, N., Riéra, B. & Charles-Dominique, P. (2008b). Above-ground biomass and productivity in a rain forest of eastern South America. *J. Trop. Ecol.*, 24, 355-366.

Chen, Y.J., Bongers, F., Cao, K.F. & Cai, Z.Q. (2008). Above- and below-ground competition in high and low irradiance: tree seedling responses to a competing liana *Byttneria grandifolia*. *J. Trop. Ecol.*, 24, 517-524.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Räisänen, Rinke, A., Sarr, A. & Whetton, P. (2007) Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Soloman, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. & Miller, H.L.). Cambridge University Press, Cambridge, UK.

Clark, D.B. & Clark, D.A. (1990). Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *J. Trop. Ecol.*, 6, 321-331.

Cleary, D.F.R & Praidjati, A. (2005). Vegetation responses to burning in a rain forest in Borneo. *Plant Ecol.*, 177, 145-163.

Cochrane, M.A. (2001). Synergistic interactions between habitat fragmentation and fire in evergreen tropical forests. *Conserv. Biol.*, 15, 1515-1521.

Cochrane, M.A. (2003). Fire science for rainforests. *Nature*, 42, 913-919.

Cochrane, M.A., Alencar, A., Schulze, M.D., Souza Jr., C.M., Nepstad, D.C., Lefebvre, P. & Davidson, E.A. (1999). Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science*, 284, 1832-1835.

Cochrane, M.A. & Laurance, W.F. (2002). Fire as a large-scale edge effect in Amazonian forests. *J. Trop. Ecol.*, 18, 311-325.

Cochrane, M.A. & Schulze, M.D. (1999) Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica*, 31, 2-16.

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

Condit, R., Aguilar, A., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S.P. & Foster, R.B. (2004). Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.*, 20, 51-72.

Condit, R., Hubbell, S.P. & Forster, R.B. (1995). Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.*, 65, 419-439.

Condit, R., Hubbell, S.P. & Forster, R.B. (1996). Changes in tree species abundance in a neotropical forest: impact of climate change. *J. Trop. Ecol.*, 12, 231-256.

Condon, M.A., Sasek, T.W. & Strain, B.R. (1992). Allocation patterns in two tropical vines in response to increased atmospheric CO_2. *Funct. Ecol.*, 6, 680-685.

Constanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. & van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253-260.

Cook, B., Zeng., N & Yoon, J.-H. (2012). Will Amazonia dry out? Magnitude and causes of change from IPCC climate model projections. *Earth Interact.*,16, 1-27.

Cox, P.M., Betts, R.A., Collins, M., Harris, P.P., Huntingford, C. & Jones, C.D. (2004). Amazon forest dieback under climate-carbon cycle projections for the 21st century. *Theor. Appl. Climatol.*, 78, 137-156.

Crutzen, P.J. (2002). Geology of mankind. *Nature*, 415, 23.

da Costa, A.C.L., Galbraith, D., Almeida, S., Portela, B.T.T., da Costa, M., de Athaydes Silva Junior, J., Braga, A.P., de Gonçalves, P.H.L., de Oliveira, A.A.R., Fisher, R., Phillips, O.L., Metcalfe, D.B., Levy, P. & Meir, P. (2010). Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazon rainforest. *New Phytol.*, 187, 579-591.

Dai, A. (2011). Drought under global warming: a review. *Wiley Interdiscip. Rev. Clim. Change*, 2, 45-65.

Darwin, C. (1867). On the movements and habits of climbing plants. *J. Linnean Soc.*, 9, 1-118.

Davidson, E.A., de Araújo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., Bustamente, M.M.C., Coe, M.T., DeFries, R.S., Keller, M., Longo, M., Nunger, J.W., Schroeder, W., Soares-Filho, B.S., Souza Jr., C.M. & Wofsy, S.C. (2012). The Amazon basin in transition. *Nature*, 481, 321-328.

Davis, C.C., Webb, C.O., Wurdack, K,J., Jaramillo, C.A. & Donoghue, M.J. (2005). Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *Am. Nat.*, 165, E36-E65.

Denslow, J.S. & DeWalt, S.J. (2008). Exotic plant invasions in tropical forests: Patterns and hypotheses. In Carson, W.P. & Schnitzer, S.A. (Eds.) *Tropical forest community ecology*. Wiley-Blackwell, Chichester.

DeWalt, S.J. & Chave, J. (2004). Structure and biomass of four lowland neotropical forests. *Biotropica*, 36, 7-19.

DeWalt, S.J., Schnitzer, S.A., Chave, J., Bongers, F., Burnham, R.J., Cai, Z., Chuyong, G., Clark, D.B., Ewango, C.E.N., Gerwing, J.J., Gortaire, E., Hart, T., Ibarra-Manríquez, G., Ickes, K., Kenfack, D., Macía, M.J., Makana, J.-R., Martínez-Ramos, M., Mascaro, J., Moses, S., Muller-Landau, H.C., Parren, M.P.E., Parthasarathy, N., Pérez-Salicrup, D.R., Putz, F.E., Romero-Saltos, H. & Thomas, D. (2010). Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, 42, 309-317.

DeWalt, S.J., Schnitzer, S.A. & Denslow, J.S. (2000). Density and diversity of liana along a chronosequence in a central Panamanian lowland forest. *J. Trop. Ecol.*, 16, 1-19.

Dillenburg, L.R., Whigham, D.F., Teramuram A.H. & Forseth, I.N. (1993). Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host Liquidambar styraciflua. *Oecologia*, 93, 48–54.

Doe, S.S.P. (2008). Fire management policy and environmental NGO movement: critical contemporary perspectives, indicators and prospects in savannas, Ghana. *GeoJournal*, 71, 159-170.

Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.T. & Hubbell, S.P. (2007). Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447, 80-82.

Enquist, B.J. & Enquist, C.A. (2011). Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. *Glob. Change Biol.*, 17, 1408-1424.

Ewango, C.E.N. (2010). *The liana assemblage of a Congolian rainforest. Diversity structure and function*. PhD Theses, Wageningen University, Wageningen, The Netherlands.

Ewers, F.W., Carlton, M.R., Fisher, J.B., Kolb, K.J. & Tyree, M.T. (1997). Vessel diameters in roots versus stems of tropical lianas and other growth forms. *IAWA J.*, 3, 261-279.

Ewers, F.W., Fisher, J.B. & Fichtner, K. (1991). Water flux and xylem structure in vines. In: *The Biology of Vines* (Eds. Putz, F.E. & Mooney, H.A.). Cambridge University Press, Cambridge.

Fairhead, J. & Leach, M. (1998). *Reframing deforestation: global analyses and local realities*. Routledge, London.

Feeley, K.J., Davies, S.J., Perez, R., Hubbell, S. & Foster, R.B. (2011). Directional changes in the species composition of a tropical forest. *Ecology*, 92, 871-882.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Areats, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., López-González, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patiño, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodt, F., Sonke, B., Taedoumg, H.E., Tan, S., White, L., Woll, H. & Lloyd, J. (2011). Height-diameter allometry of tropical forest trees. *Biogeosciences*, 8, 1081-1106.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, E., Monteagudo Mendoza, A. López-González, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., C, G.A.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Dávila, E.A., de Oliveira, A., DiFiore, A., Djagbletey, G., Domingues, T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., C, E.H., Iida, Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.H., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V., White, L., Wilcock, S., Woell, H. & Phillips, O.L. (2012). Tree height integrated into pan-tropical forest biomass estimates. *Biogeosciences Discuss.*, 9, 2567-2622.

Field, C.B. & Holbrook, N.M. (1989). Catastrophic xylem failure: tree life at the brink. *Trends Ecol. Evol.*, 4, 124-126.

Fine, P.V.A. (2002). The invisibility of tropical forests by exotic plants. *J. Trop. Ecol.*, 18, 687-705.

Fisher, J.B. & Ewers, F.W. (1991). Structural responses to stem injury in vines. In: *The Biology of Vines* (Eds. Putz, F.E. & Mooney, H.A.). Cambridge University Press, Cambridge.

Fisher, R.A, Williams, M., da Costa, A.L., Malhi, Y., da Costa, R.F., Almeida, S. & Meir, P. (2007). The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Glob. Change Biol.*, 13, 2361-2378.

Fisher, R.A, Williams, M., Lobo de Vale, R., da Costa, A.L., & Meir, P. (2006). Evidence from Amazon forests is consistent with isohydric control of leaf water potential. *Plant Cell Environ.*, 29, 151-165.

Flores, O. & Coomes, D.A. (2006). Estimating the wood density of species for carbon stock assessments. *Method. Ecol. Evol.*, 2, 214-220.

FORIG (2003). Final technical report: forest fire management in Ghana. Forestry Research Institute of Ghana, Kumasi.

Foster, J.R., Townsend, P.A. & Zganjar, C.E. (2008). Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. *Remote Sens. Environ.*, 112, 2104-2117.

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 dynamics global vegetation models under climate change. *New Phytol.*, 187, 647-665.

Gentry, A.H. (1991). The distribution and evolution of climbing plants. In: *The Biology of Vines* (Eds. Putz, F.E. & Mooney, H.A.). Cambridge University Press, Cambridge.

Gerwing, J.J. (2002). Degradation of forests through logging and fire in the eastern Brazilian Amazon. Forest Ecol. Manag., 157, 134-141.

Gerwing, J.J. & Farias, D.L. (2000). Integrating liana abundance and forest stature into an estimate of total aboveground biomass for an eastern Amazonian forest. *J. Trop. Ecol.*, 16, 327-335.

Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N,m Foster, R., Kenfack, D., Martínez-Ramos, M., Parren, M., Parthasarathy, N., Pérez-Salicrup. D.R., Outz, F.E. & Thomas, D.W. (2006). A standard protocol for liana censuses. *Biotropica*, 38, 256-261.

Giglio, L., Descloitres, J., Justice, C.O. & Kaufman, Y.J. (2003). An enhanced contextual fire detection algorithm for MODIS. *Remote. Sens. Environ.*, 87, 273-282.

Goldammer, J.G. & Seibert, B. (1989). natural rain forest fires in Eastern Borneo during the Pleistocene and Holocene. *Naturwissenschaften*, 76, 518-520.

Gould, K.A., Fredericksen, T.S., Morales, F., Kennard, D., Putz, F.E., Mostacedo, B. & Toledo, M. (2002). Post-fire tree regeneration in lowland Bolivia: implications for fire management. *Forest Ecol. Manag.*, 165, 225-234.

Granados, J. & Körner, C. (2002). In deep shade, elevated CO_2 increases the vigor of tropical climbing plants. *Glob. Change Biol.*, 8, 1109-1117.

Grainger, A., Boucher, D.H., Frumhoff, P.C., Laurance, W.F., Lovejoy, T., McNeely, J., Miekisch N., Raven, P., Sodhi, N.S., Venter, O. & Pimm, S.L. (2009). Biodiversity and REDD at Copenhagen. *Curr. Biol.*, 19, R974-R976.

Gutsell, S.L. & Johnson, E.A. (1996). How fire scars are formed: coupling a disturbance process to its ecological effect. *Can. J. Forest Res.*, 26, 166-174.

Hall, J.B. & Swaine, M.D. (1976). Classification and ecology of closed-canopy forest in Ghana. *J. Ecol.*, 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, The Hague.

Hammond, D.S. & ter Steege, H. (1998). Propensity for fires in Guianan rainforests. *Conserv. Biol.*, 12, 944-947.

Hawthorne, W.D. (1995). *Ecological profiles of Ghanaian forest trees.* Oxford Forestry Institute, Oxford.

Hawthorne, W.D. & Abu Juam, M. (1995). *Forest Protection in Ghana.* IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Hegarty, E.E. & Caballé, G. (1991). Distribution and abundance of vines in forest communities. In: *The Biology of Vines* (Eds. Putz, F.E. & Mooney, H.A.). Cambridge University Press, Cambridge.

Hendriks, M.R. (2010). *Introduction to Physical Hydrology*. Oxford University Press, Oxford, UK.

Henry, M., Besnard, A., Asante, W.A., Eshun, J., Adu-Bredu, S., Valentini, R., Bernoux, M. & Saint-André, L. (2010). Wood density, phytomass variations within and among trees, and allometric equations in a tropical rainforest of Africa. *Forest Ecol. Manag.*, 260, 1375-1388.

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. *Int. J. Climatol.*, 25, 1965-1978.

Hochberg, Y. (1988). A sharper Bonferroni procedure for multiple tests of significance. *Biometrika*, 75, 800 – 802.

Holdsworth, A.R. & Uhl, C. (1997). Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecol. Appl.*, 7, 713-725.

Horn, S.P. & Sanford, R.L. (1992). Holocene fires in Costa Rica. *Biotropica*, 24, 354-361.

Hu, L., Li, M & Li, Z. (2010). Geographical and environmental gradients of lianas and vines in China. *Global Ecol. Biogeog.*, 19, 554-561.

Ichihashi, R. & Tateno, M. (2011). Strategies to balance between light acquisition and the risk of falls of four temperate liana species: to overtop host canopies or not? *J. Ecol.*, 99, 1071-1080.

Ingwell, L.L., Wright, S.J., Becklund, K.K., Hubbell, S.P. & Schnitzer, S.A. (2010). The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *J. Ecol.*, 98, 879-887.

Jiménez-Castillo, M. & Lusk, C.H. (2009). Host infestation patterns if the massive liana Hydrangea serratigoli (Hydrangeeaceae) in a Chilean temperate rainforest. *Austral Ecol.*, 34, 829-834.

Johns, A. (1988). Effects of “selective” timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica*, 20, 31-37.

Kalame, F.B., Nkem, J., Idinoba, M. & Kanninen, M. (2009). Matching national forest policies and management practices for climate change adaptation in Burkina Faso and Ghana. *Mitigation Adaptation Strategies Glob. Change*, 14, 135-151.

Kapos, V. (1989). Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.*, 5, 173-185.

Kariuki, M., Kooyman, R.M., Smith, R.G.B., Wardell-Johnson, G. & Vanclay, J.K. (2006). Regeneration changes in tree species abundance, diversity and structure in logged and unlogged subtropical rainforest over a 36-year period. *Forest Ecol. Manag.*, 236, 162-176.

King, D.A., Davies, S.J., Tan, S. & Noor, N.S.M.D. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *J. Ecol.*, 94, 670-680.

Lapola, D.M., Oyama, M.D. & Nobre, C.A. (2009). Exploring the range of climate biome projections for tropical South America: The role of CO_2 fertilization and seasonality. *Global Biogeochem. Cy.*, 23, 1-16.

Laurance, W.F. (2006). Fragments and fire: alarming synergisms among forest disturbance, local climate change, and burning in the Amazon. In Laurance, W.F. & Peres, C.A. (Eds.) *Emerging threats to tropical forests*. The University of Chicago Press, Chicago.

Laurance, W.F. (2007). A new initiative to use carbon trading for tropical forest conservation. *Biotropica*, 39, 20-24.

Laurance, W.F., Ferreira, L.V., Rankin-de Merona, J.M. & Laurance, S.G. (1998). Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology*, 79, 2032-2040.

Laurance, W.F., Goosem, M. & Laurance, S.G.W. (2009). Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.*, 24, 659-669.

Laurance, W.F., Laurance, S.G., Ferreira, L.V., Tankin-de Merona, J.M., Gascon, C. & Lovejoy, T.E. (1997). Biomass collapse in Amazonian forest fragments. *Science*, 278, 1117-1118.

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P., Lovejoy, T.E., Condit, R., Chave, J., Harms, K.E. & D'Angelo, S. (2006). Rapid decay of tree-community composition in Amazonian forest fragments. *PNAS*, 103, 19010-19014.

Laurance, W.F., Oliveira, A.A., Laurance, S.G., Condit, R., Nascimento, H.E.M., Sanchez-Thorin, A.C., Lovejoy, T.E., Andrade, A., D'Angelo, S., Ribeiro, J.E. & Dick, C.W. (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171-175.

Laurance, W.F., & Peres, C.A. (eds.) (2006). *Emerging threats to tropical forests*. The University of Chicago Press, Chicago.

Laurance, W.F., Pérez-Salicrup, D., Delamônia, P., Fearnside, P.M., D'Angelo. S., Jerozolinski, A., Pohl, L. & Lovejoy, T.E. (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*, 82, 105-116.

Legendre, P. & Gallagher, E.D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129, 271-280.

Leighton, M. & Wirawan, N. (1986). Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982-83 El Niño Southern Oscillation event. In Prance, G.T. (Ed.). *Tropical rain forests and the world atmosphere*. AAAS Symposium 10, Boulder, Colorado.

Lewis, S.L. (2006). Tropical forests and the changing earth system. *Philos. T. Roy. Soc. B.*, 361, 195-210.

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

Lewis, S.L., Lloyd, J., Sitch, S., Mitchard, E.T.A. & Laurance, W.F. (2009b). Changing ecology of tropical forests: Evidence and drivers. *Annu. Rev. Ecol. Evol. Syst.*, 40, 529-549.

Lewis, S.L., López-González, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo K., M.-N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.-R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.-H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R. & Wöll, H. (2009a). Increasing carbon storage in intact African tropical forests. *Nature*, 457, 1003-1006.

Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Torres Lezama, A., Vásquez Martinez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P. & Vinceti, B. (2004). Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Phil. Trans. R. Soc. B.*, 359, 421-436.

Llorens, A.M. & Leishman, M.R. (2008). Climbing strategies determine light availability for both vines and associated structural hosts. *Aust. J. Bot.*, 56, 527-534.

López-González, G., Lewis, S.L., Burkitt, M., Phillips, O.L. (2011a). *Forest Plots Database*. Available at: www.ForestPlots.net

López-González, G., Lewis, S.L., Burkitt, M., Phillips, O.L. (2011b). ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data. *J. Veg. Sci.*, 22, 610-613.

Madeira, B.G., Espírito-Santo, M.M., D'Angelo Neto, Nunes, Y.R.F., Sánchez Azofeifa, G.A., Fernandes, G.W. & Quesada, M. (2009). Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecol.*, 201, 291-304.

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.

Maley, J. (1991). The African rain forest vegetation and palaeoenvironments during late quaternary. *Climatic Change*, 19, 78-98.

Malhi, Y. & Wright, J. (2004). Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philos. T. Roy. Soc. B*, 359, 311-329.

Malhi, Y., Aragão, L.E.O.C., Galbraith, D., Hungtinford, 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. *P. Natl. Acad. Sci.*, 106, 20610-20615.

Marengo, J. (2009). Climate change and hydrological modes of the wet tropics. In Bush, M.B. & Flenley, J.R. (Eds.) *Tropical rainforest responses to climatic change*. Praxis Publishing Ltd, Chichester.

Marengo, J.A., Nobre, C.A., Tomasella, J., Oyama, M.D., de Oliveira, G.S., de Oliveira, R., Camargo, H., Alves, L.M., & Brown, I.F. (2008). The drought of Amazonia in 2005. *J Climate*, 21, 496-516.

Mayaux, P., Holmgren, P., Achard, F., Eva, H., Stibig, H.-J. & Branthomme, A. (2005). Tropical firest cover change in the 1990s and options for future monitoring. *Phil. Trans. R. Soc. B.*, 360, 373-384.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K. & Stitt, M. (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Treds Ecol. Evol.*, 26, 523-532.

McDowell, N.G. & Sevanto, S. (2010). The mechanisms of carbon starvation: how, when, or does it even occur at all? *New Phytol.*, 186, 264-266.

McGregor, G.R. & Nieuwolt, S. (1998). *Tropical Climatology*. John Wiley & Sons, Chichester.

Metcalfe, D.B., Lobo-do-Vale, R., Chaves, M.M., Maroco, J.P., Aragão, L.E.O.C., Malhi, Y. da Costa, A.L., Braga, A.P., Gonçalves, P.H.L., de Athaydes, J., da Costa, M., Almeida, S.S., Campbell, C., Hurry, V., Williams, M. & Meir, P. (2010b). Impacts of experimentally imposed drought on leaf respiration and morphology in an Amazon rain forest. *Funct. Ecol.*, 24, 524-533.

Metcalfe, D.B., Meir, P., Aragão, L.E.O.C., Lobo-do-Vale, R., Galbraith, D., Fisher, R.A., Chaves, M.M., Maroco, J.P., da Costa, A.C.L., de Almeida, S.S., Braga, A.P., Gonçalves, P.H.L., de Athaydes, J., da Costa, M., Portela, T.T.B., de Oliveira, A.A.R., Malhi, Y. & Williams, M. (2010b). Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon. *New Phytol.*, 187, 608-621.

Mitchell, T.D. & Jones, P.D. (2005). An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.*, 25, 693-712.

MLFM (2006). National Wildfire Management Policy. Ministry of Lands, Forestry and Mines, Accra.

Muoghalu, J.I. (2006). Tree species population dynamics in a secondary forest at Ile-Ife, Nigeria after a ground fire. *Afr.J. Ecol.*, 45, 62-71.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.

Nabe-Nielsen, J. (2001). Diversity and distribution of lianas in a neotropical rain forest, Yasuni National Park, Ecuador. *J. Trop. Ecol.*, 17, 1-19.

Nabe-Nielsen, J., Kollmann, J. & Peña-Claros, M. (2009). Effects of liana load, tree diameter and distances between conspecifics on seed production in tropical timber trees. *Forest Ecol. Manag.*, 257, 987-993.

Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T., Sato, K., Miguchi, H., Nagamasu, H., Ogino, K., Teo, S., Hamid, A.A. & Seng, L.H. (2000). Impact of severe drought associated with the 1997-1998 El Niño in a tropical forest in Sarawak. *J. Trop. Ecol.*, 16, 355-367.

Nasi, R., Wunder, S., Campos A., J.J. (2002*). "Forest ecosystem services: Can they pay our way out of deforestation?".* CIFOR for the Global Environmental Facility (GEF), Bogor, Indonesia.

Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., da Silva, E.D., Stone, T.A., Trumbore, S.E. & Vieira, S. (1994). The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature, 372, 666-669.

Nepstad. D.C., Moutinho, P., Dias-Filho, M.B., Davidson, E., Cardinot, G., Markewitz, D., Figueiredo, R., Vianna, N., Chambers, J., Ray, D., Guerreiros, J.B., Lefebvre, P., Sternberg, L., Moreira, M., Barros, L., Ishida, F.Y., Tohlver, I., Belk, E., Kalif, K. & Schwalbe, K. (2002). The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. *J. Geophys. Res.*, 107, LBA 53, 1-17.

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.

Nesheim, I. & Økland, R.H. (2007). Do vine species in neotropical forests see the forest or the trees? *J. Veg. Sci.*, 18, 395-404.

Nevle, R.J. & Bird, D.K. (2008). Effects of syn-pandemic fire reduction and reforestation in the tropical Americas on atmospheric CO_2 during European conquest. *Palaeogeogr. Palaeocl.*, 264, 25-38.

Newbery, D.M., Lingenfelder, M., Poltz, K.F., Ong, R.C. & Ridsdale, C.E. (2011). Growth responses of understorey trees to drought perturbation in tropical rainforest in Borneo. *Forest Ecol. Manag.*, 262, 2095-2107.

Nicholson, S.E., Some, B. & Kone, B. (2000). An analysis of recent rainfall conditions in west africa, including the rainy seasons of the 1997 El Niño and the 1998 La Niña years. *J. Climate*, 13, 2628-2640.

Nielsen, M.S. (1965). *Introduction to the Flowering Plants of West Africa*. University of London Press, London.

Nogueira, A., Costa, F.R.C. & Castilho, C.V. (2011). Liana abundance patterns: the role of ecological filters during development. *Biotropica*, 43, 442-449.

Numata, I., Cochrane, M.A. & Galvão, L.S. (2011). Analyzing the impacts of freguency and severity of forest fire on the recovery of disturbed forest using Landsat time series and EO-1 Hyperion in the southern Brazilian Amazon. *Earth Interact.*,15, 1-17.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, M., Stevens, H.H. & Wagner, H. (2011). vegan: Community Ecology Package. R package version 2.0-0. http://CRAN.R-project.org/package=vegan

Oliveira, R.S., Dawson, T.E., Burgess, S.S.O. & Nepstad, D.C. (2005). Hydraulic redistribution in three Amazonian trees. *Oecologia*, 145, 354-363.

Owusu, K. & Waylen, P. (2009). Trends in spatio-temporal variability in annual rainfall in Ghana (1951-2000). *Weather*, 64, 115-120.

Padaki, A. & Parthasarathy, N. (2000). Abundance and distribution of lianas in tropical lowland evergreen forest of Agumbe, central Western Ghats, India. *Trop. Ecol.*, 41, 143-154.

Paine, C.E.T., Stahl, C., Courtois, E.A., Patiño, S., Sarmiento, C. & Baraloto, C. (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. *Funct. Ecol.*, 24, 1202-1210.

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.

Parthasarathy, N., Muthuramkumar, S., Sridhar Reddy, M. (2004). Patterns of liana diversity in tropical evergreen forests of peninsula India. *Forest Ecol. Manag.*, 190, 15-31.

Penalosa, J. (1984). Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica*, 16, 1-9.

Peres, C.A., Barlow, J. & Laurance, W.F. (2006). Detecting anthropogenic disturbance in tropical forests. *Trends Ecol. Evol.*, 21, 227-229.

Pérez-Salicrup, D.R. & de Maijere, W. (2005). Number of lianas per tree and number of trees climbed by lianas at Los Tuxtlas, Mexico. *Biotropica*, 37, 153-156.

Pérez-Salicrup, D.R. & Barker, M.G. (2000). Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia*, 124, 469-475.

Pérez-Salicrup, D.R., Sork, V.L. & Putz, F.E. (2001). Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica*, 33:34-47.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G. Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., Cristina Alves de Oliveira, Á., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Thomas, A.S., ter Steege, H., Stropp, J., Váaquez, R., Zelazowski, P., Alvarez Dávila, E., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., Honorio C., E., Keeling, H., Killeen, T.J., Laurance, W.F., Peña Cruz, A., Pitman, N.C.A., Núñez Vargas, P., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J. & Torres-Lezama, A. (2009a). Drought sensitivity of the Amazon Rainforest. *Science*, 323, 1344-1347.

Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez-Vargas, P., Silva, J.N.M., Terborgh, J., Vásquuez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A. & Vinceti, B. (2004). Pattern and process in Amazon tree turnover, 1976-2001. *Phil. Trans. R. Soc. B.*, 359, 381-407.

Phillips, O.L., Baker, T.R., Feldpausch, T.R. & Brienen, R. (2009b). RAINFOR field manual for plot establishment and remeasurement. Available at: http://www.geog.leeds.ac.uk/projects/rainfor/pages/manuals_eng.html. Last accessed 15 September 2011.

Phillips, O.L. & Gentry, A.H. (1994). Increasing turnover through time in tropical forests. *Science*, 263, 954-958.

Phillips, O.L., Martinez, R.V., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Núñez vargas, P., Alexiades, M., Cerón, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vinceti, B. (2002). Increasing dominance of large lianas in Amazonian forests. *Nature*, 418, 770-774.

Phillips, O.L., Martinez, R.V., Mendoza, A.M., Baker, T.R. & Vargas, P.N. (2005). Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, 86, 1250-1258.

Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Núñez, P.V., Vásquez, R.M., Laurance, S.G., Ferreira, L.V., Stern, M., Brown, S. & Grace, J. (1998). Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science*, 282, 439-442.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragao, L.E.O.C, Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Alvarez Da´vila E., Amaral, I., Andelman, S., Andrade, A., Arroyo L., Aymard, G., Baker, T.R., Blanc, L., Bonal D., Cristina Alves de Oliveira, A., Chao K.-J., Da´vila Cardozo N., da Costa, L., Feldpausch, T.R., Fisher J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jiménez E., Keeling, H., Killeen T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel C., Núñez Vargas, P., Patiño, S., Peh, K.S-H., , Peña Cruz, A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira M., Slik J.W.F., Sonké, B., Sota Thomas, A., Stropp, J., Taplin, J.R.D., Vásquez, R. & Vilanova, E. (2010). Drought-mortality relationships for tropical forests. *New Phytol.*, 187, 631-646.

Pinard, M.A. & Huffman, J. (1997). Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *J. Trop. Ecol.*, 13, 727-740.

Pinard, M.A., Putz, F.E. & Licona, J.C. (1999). Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *Forest Ecol. Manag.*, 116, 247-252.

Pleysier, J.L. & Juo, A.S.R. (1980) A single-extraction method using silver-thiourea for measuring exchangeable cations and effectice cec in soils with variable charges. Soil Sci., 129, 205-211.

Poorter, L., Bongers, F., Kouame, F.N'. & Hawthrone, W.D. (eds.) (2004). *Biodiversity of West African Forests: An ecological atlas of woody plant species*. CABI Publishing, Wallingford.

Poorter, L., Hawthorne, W., Bongers, F. & Sheil, D. (2008). Maximum size distributions in tropical forests communities: relationships with rainfall and disturbance. *J. Ecol.*, 96, 495-504.

Potts, M.D. (2003). Drought in a Bornean everwet rain forest. *J. Ecol.*, 91, 467-474.

Putz, F.E. (1983). Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro basin, Venezuela. *Biotropica,* 15, 185-189.

Putz, F.E. (1984a). The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, 65, 1713-1724.

Putz, F.E. (1984b). How trees avoid and shed lianas. *Biotropica*, 16, 19-23.

Putz, F.E. & Chai, P. (1987). Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.*, 75, 523-531.

Putz, F.E. & Holbrook, N.M. (1991). Biomechanical studies of vines. In: *The Biology of Vines* (Eds. Putz, F.E. & Mooney, H.A.). Cambridge University Press, Cambridge.

Putz, F.E. & Windsor, D.M. (1987). Liana phenology on Barro Colorado Island, Panama. *Biotropica*, 19, 334-341.

Quesada, C.A., Lloyd, J., Schwarz, M., Patiño, S., Baker, T.R., Czimczik, C., Fyllas, N.M., Martinelli, L., Nardoto, G.B., Schmerler, J., Santos, A.J.B., Hodnett, M.G., Herrera, R., Luizão, F.J., Lloyd, G., Dezzeo, N., Hilke, I., Kuhlmann, I., Raessler, M., Brand, W.A., Geilmann, H., Moraes Filho, J.O., Araujo, R.N., Chaves, J.E., Cruz Junior, O.F., Pimentel, T.P. & Paiva, R. (2010). Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences*, 7, 1515-1541.

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Reddy, M.S. & Partharathy, N. (2003). Liana diversity and distribution in four tropical dry evergreen forests on the Coromandel coast of south India. *Biodivers. Conserv.*, 12, 1609-1627.

Restom, T.G., Nepstad, D.C. (2001). Contribution of vines to the evapotranspiration of a secondary forest in eastern Amazonia. *Plant Soil,* 236, 155–163

Román-Cuesta, R.M., Salinas, N., Asbjornsen, H., Oliveras, I., Huaman, V., Gutiérrez, Y., Puelles, L., Kala, J., Yabar, D., Rojas, M., Astete, R., Jordán, D.Y., Silman, M., Mosandl, R., Weber, M., Stimm, B., Günter, S., Knoke, T. & Malhi, Y. (2011). Implications of fires on carbon budgets in Andean cloud montane forest: The importance of peat soils and tree resprouting. *Forest Ecol. Manag.*, 261, 1987-1997.

Sala, A., Piper, F. & Hoch, G. (2010). Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytol.*, 186, 274-281.

Salinger, M.J. (2005). Climate variability and change: past, present and future - an overview. *Climatic Change*, 70, 9-29.

Sanford, R.L., Saldarriaga, J., Clark, K.E., Uhl, C. & Herrera, R. (1985). Amazon rain-forest fires. *Science*, 227, 53-55.

Schnitzer, S.A. (2005). A mechanistic explanation of global patterns of liana abundance and distribution. *Am. Nat.*, 116, 262-275.

Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends Ecol. Evol.*, 17, 223-230.

Schnitzer, S.A. & Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol. Let.*, 14, 397-406.

Schnitzer, S.A. & Carson, W.P. (2001) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, 82, 913-919.

Schnitzer, S.A., Dalling, J.W. & Carson W.P. (2000). The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J. Ecol.*, 88, 655-666.

Schnitzer, S.A., Kuzee, M.E. & Bongers, F. (2005). Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *J. Ecol.*, 93, 1115-1125.

Shanahan, T.M., Overpeck, J.T., Anchukaotos, K.J., Beck, J.W., Cole, J.E., Dettman, D.L. Peck, J.A., Scholz, C.A. & King, J.W. (2009). Atlantic forcing of persistent drought in West Africa. *Science*, 74, 377-380.

Shaw, E.M. (1994). *Hydrology in Practice.* 3rd Edition. Chapman & hall, London, UK.

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

Shuttleworth, W.J. (1989). Micrometeorology of temperate and tropical forest. *Phil. Trans. R. Soc. B.*, 324, 299-334.

Silvestrini, R.A., Soares-Filho, B.S., Nepsatd, D., Coe, M., Rodrigues, H. & Assuncao, R. (2011). Simulating fire regimes in the Amazon in response to climate change and deforestation. *Ecol. Appl.*, 21, 1573-1590.

Sizer, N.C., Tanner, E,V.J. & Kossman Ferraz, I. (2000). Edge effects on litterfall mass and nutrient concentrations in fragments in central Amazonia. *J. Trop. Ecol.*, 16, 853-863.

Slik, F.W.F. (2004). El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia*, 141, 112-120.

Slik, J.W.F., Bernard, C.S., Van Beek, M., Breman, F.C. & Eichhorn, K.A.O. (2008). Tree diversity, composition, forest structure and aboveground biomass dynamics after single and repeated fire in a Bornean rain forest. *Oecologia*, 158, 579-588.

Slik, J.W.F., Breman, F.C., Bernard, C., van Beek, M., Cannon, C.H., Eichhorn, K.A.O. & Sidiyasa, K. (2010). Fire as a selective force in a Bornean tropical everwet forest. *Oecologia*, 164, 841-849.

Slik, J.W.F. & Eichhorn, K.A.O. (2003). Fire survival of lowland tropical rain forest trees in relation to stem diameter and topographic position. *Oecologia*, 137, 446-455.

Slik, J.W.F., Verburg. R.W. & Keβler, P.J.A. (2002). Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia. *Biodivers. Conserv.*, 11, 85-98.

Soares-Filho, B., Silvestrini, R., Nepstad, D.C., Brando, P., Rodrigues, H., Alencar, A., Coe, M., Locks, C., Lima, L., Hissa, L. & Stickler, C. (2012). Forest fragmentation, climate change and understory fire regimes on the Amazonian landscapes of the Xingu headwaters. *Landscape Ecol.*, 27, 585-598.

Swaine, M.D. (1992). Characteristics of dry forest in West Africa and the influence of fire. *J. Veg. Sci.*, 3, 365-374.

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

Swaine, M.D., Agyeman, V.K., Kyereh, B., Orgle, T.K., Thompson, J. & Veenendaal, E.M. (1997) *Ecology of forest trees in Ghana*. ODA Forestry Series No. 7, University of Aberdeen, Aberdeen.

Swaine, M.D. & Grace, J. (2007). Lianas may be favoured by low rainfall: evidence from Ghana. *Plant Ecol.*, 192, 271-276.

Swaine, M.D., Hall, J.B. & Alexander, I.J. (1987). Tree population dynamics at Kade, Ghana (1968-1982). *J. Trop. Ecol.* 3, 331-345.

Talley, S.M., Setzer, W.N. & Jackes, B.R. (1996). Host associations of two adventitious-root-climbing vines in a North Queensland tropical rain forest. *Biotropica*, 28, 356-366.

Tang, Y., Kitching, R.L. & Cao, M. (2012). Lianas as structural parasites: A re-evaluation. *Chinese Sci. Bull.*, 57, 307-312.

Terborgh, J., Nuñez-Iturri, G., Pitman, N.C.A., Cornejo Valverdem F.H., Alvarez, P., Swamy, V., Pringle, E.G. & Paine, C.E.T. (2008). Tree recruitment in an empty forest. *Ecology*, 89, 1757-1768.

Tiessen, H. & Moir, J.O. (1993). Total and organic carbon. In: Soil Sampling and Methods of Analysis (Ed. Carter, M.R). Leis Publ. Boca Raton, Florida.

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C. & Bongers, F. (2011). Climate and soil drive forest structure in Bolivian lowland forests. *J. Trop. Ecol.*, 27, 333-345.

Toledo-Aceves, T. & Swaine, M.D. (2008). Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. *Plant Ecol.*, 196, 233-244.

Tyree, M.T. & Ewers, F.W. (1991). The hydraulic architecture of trees and other woody plants. *New Phytol.*, 119, 345-360.

Uhl, C. & Buschbacher, R. (1985). A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the eastern Amazon. *Biotropica*, 17, 265-268.

Uhl, C. & Kauffman, J.B. (1990). Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology*, 71, 437-449.

Uhl, C., Kauffman, J.B. & Cummings, D.L. (1988). Fire in the Venezuelan Amazon 2: environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos*, 53, 176-184.

van der Heijden, G.M.F., Feldpausch, T.R., de la Fuente Herrero., A., van der Velden, N.K. & Phillips, O.L. (2010). Calibrating the liana crown occupancy index in Amazonian forests. *Forest Ecol. Manag.*, 260, 549-555.

van der Heijden, G.M.F., Healey. J.R. & Phillips, O.L. (2008) Infestation of trees by lianas in a tropical forest in Amazonian Peru. *J. Veg. Sci.*, 19, 747-756.

van der Heijden, G.M.F. & Phillips, O.L. (2008). What controls liana success in Neotropical forests? *Global Ecol. Biogeog.*, 17, 372-383.

van der Heijden, G.M.F. & Phillips, O.L. (2009a). Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, 6, 2217-2226.

van der Heijden, G.M.F. & Phillips, O.L. (2009b). Environmental effects on Neotropical liana species richness. *J. Biogeogr.*, 8, 1561-1572.

van der Molen, M.K., Dolman, A.J., Ciais, P., Eglin, T., Gobron, N., Law, B.E., Meir, P., Peters, W., Phillips, O.L., Reichstein, M., Chen, T., Dekker, S.C., Doubková, M., Friedl, M.A., Jung, M., van den Hurk, B.J.J.M., de Jeu, R.A.M., Krujit, B., Ohta, T., Rebel, K.T., Plummer, S., Seneviratne, S.I., Sitch, S., Teuling, A.J., van der Werf, G.R. & Wang, G. (2011). Drought and ecosystem carbon cycling. *Agr. Forest Meteorol.*, 151, 765-773.

van Nieuwstadt, M.G.L. & Sheil, D. (2005). Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. *J. Ecol.*, 93, 191-201.

Van Wagner, C.E. (1973). Height of crown scorch in forest fires. *Can. J. Forest. Res.*, 3, 373 - 378.

Vargas, R., Allen, M.F. & Allen. E.B. (2008). Biomass and carbon accumulation in a fire chronosequence of a seasonally dry tropical forest. *Global Change Biol.*, 14, 109-124.

Verburg, R. & van Eijk-Bos, C. (2003). Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *J. Veg.Sci.*, 14, 99-110.

Walker, B., Holling, C.S., Carpenter, S.R. & Kinzig, A. (2004). Resilience, adaptability and transformability in social-ecological systems. *Ecol. Soc.*, 9, 5.

Wang, R.L., Zeng, R.S., Peng, S.L., Chen, B.M., Liang, X.T. & Xin, X.W. (2011). Elevated temperature may accelerate invasive expansion of the liana plant *Ipomoea cairica*. *Weed Res.*, 51, 574-580.

Williamson, G.B., Laurance, W.F., Oliveira, A.A., Delamônica, P., Gascon, C., Lovejoy, T.E. & Pohl, L. (2000). Amazonian tree mortality during the 1997 El Niño drought. *Conserv. Biol.*, 14, 1538-1542.

Wong, J.L.G. (1996). Inventory for forest management planning: Experience in Ghana. In IUFRO conference on growth studies in moist tropical forests in Africa, Kumasi, Ghana, 11-15 Nov 1996, Forestry Research Institute of Ghana, Kumasi.

Woods, P. (1989). Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica*, 21, 290-298.

Wright, S.J. & Calderon, O. (2006). Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.*, 9, 35-44.

Wright, S.J., Calderon, O., Hernandez, A. & Paton, S. (2004). Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology*, 85, 484-489.

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

Wright, S.J., Hernandéz, A. & Condit, R. (2007). The bushmeat harvest alters seedling banks by favouring lianas, large seeds, and seeds dispersed by bats, birds and wind. *Biotropica*, 39, 363-371.

Yuan, C.M., Liu, W.Y., Tang, C.Q. & Li, Z.S. (2009). Species composition, diversity, and abundance of lianas in different secondary and primary forests in a subtropical mountainous area, SW China. *Ecol. Res.*, 24, 1361-1370.

Zalasiewicz, J., Williams, M., Haywood, A., & Ellis, M. (2011). The anthropocene: a new epoch of geological time? *Philos. T. R. Soc. A.*, 369, 835-841.

Zanne, A.E., López-González, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C. & Chave, J. (2009). Global wood density database. Available at: http://hdl.handle.net/10255/dryad.235.

Zhu, S.-D. & Cao, K.-F. (2010). Contrasting cost-benefit strategy between lianas and trees in a tropical seasonal rain forest in southwestern China. *Oecologia*, 163, 591-599.

Zhu, S.-D. & Cao, K.-F. (2009). Hydraulic properties and photosynthetic rates in co-occurring lianas and trees in a seasonal tropical rainforest in southwestern China. *Plant Ecol.*, 204, 295-304.

List of Abbreviations

AFRITRON	African Tropical Rainforest Observation Network
Ag-TU	Silver Thiourea
AIC	Akaike Information Criterion
AIC_c	Second order Akaike Information Criterion
Al	Aluminium
ANOVA	Analysis of variance
BCI	Barro Colorado Island
BP	Years before present
C	Carbon
Ca	Calcium
CI	Confidence interval
CO_2	Carbon dioxide
CPTEC	Centro de Previsão de Tempo e Estudos Climáticos
CRU	Climate Research Unit
D	Diameter at 1.3 m or above buttresses
DCA	Detrended correspondence analysis
DGVM	Dynamic global vegetation model
D*max*	Maximum diameter below 2.5 m
ECEC	Effective cation exchange capacity
ENSO	El Niño Southern Oscillation
FCG	Forestry Commission of Ghana
FORIG	Forestry Research Institute of Ghana
GCM	Global climate model
GPP	Gross primary productivity
H	Height
ICP-OES	Inductively coupled plasma optical emission spectroscopy
INPE	National Institute for Space Research
IPCC	Intergovernmental Panel on Climate Change

IPCC-AR4	IPCC Fourth Assessment Report
ITCZ	Intertropical convergence zone
K	Potassium
MAP	Mean annual precipitation
MCWD	Maximum cumulative water deficit
MFLM	Ministry of Lands, Forestry and Mines
Mg	Magnesium
ML	Maximum likelihood
MODIS	Moderate-resolution Imaging Spectroradiometer
N	Nitrogen
Na	Sodium
NMDS	Non-metric multidimensional scaling
NPLD	Non-pioneer light demander
P	Phosphorus
PCA	Principal components analysis
pp	Percentage point
POM	Point of measurement
PSP	Permanent sample plot
REDD+	Reduced Emissions from Deforestation and Forest Degradation
REML	Restricted maximum likelihood
sd	Standard deviation
TFE	Throughfall exclusion
TROBIT	Tropical Biomes in Transition
ρ	Wood density

Appendix

Table A1. Plot level trait changes based on stem numbers. All values are annual rates of change. For categorical variables Rel. = change in percentage of trees of that trait (percentage point yr^{-1}) and Abs. = change in stem numbers (stems ha^{-1} yr^{-1}) of trees with that trait. Bootstrapped mean weighted by plot size and 95% CI are given for each trait. Significant changes across all plots are in bold.

Plot	Habitat Score (units yr^{-1})	Wood Density (g cm^{-3} yr^{-1})	Deciduous		Pioneers		NPLD		Shade Bearers		Understorey		Sub-canopy		Canopy	
			Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.
ASN-02	0.175	0.00028	-0.027	-0.288	-0.039	-0.288	-0.081	-0.577	0.120	0.000	0.082	0.288	-0.187	-1.010	0.105	-0.072
ASN-04	-0.041	-0.00027	0.034	-0.072	-0.017	-0.144	0.028	-0.072	-0.011	-0.289	0.101	0.361	-0.205	-1.083	0.104	0.144
BBR-14	0.815	-0.00058	-0.065	-0.202	-0.076	-0.304	0.335	1.568	-0.259	-1.012	-0.095	-0.405	0.294	1.315	-0.200	-0.809
BBR-16	0.180	0.00018	0.023	1.163	-0.123	-0.051	0.207	2.680	-0.086	0.809	-0.105	-0.354	0.006	1.011	0.099	2.275
BBR-17	0.858	-0.00007	0.140	1.719	-0.202	-0.491	0.492	3.193	-0.290	-0.589	-0.046	-0.098	0.092	0.884	-0.045	1.277
BOR-05	0.232	-0.00071	0.039	1.054	-0.031	0.246	0.214	1.922	-0.183	0.930	-0.057	0.000	-0.125	1.426	0.182	2.170
BOR-06	0.590	-0.000002	-0.069	0.377	0.087	0.627	-0.027	0.816	-0.060	1.318	0.021	0.251	0.132	2.762	-0.154	0.314
CAP-09	-0.129	0.00008	-0.016	-0.072	-0.034	-0.143	-0.066	-0.215	0.099	1.073	0.068	0.358	0.064	0.787	-0.132	-0.358
CAP-10	-0.327	0.00214	0.255	1.357	0.012	0.214	0.085	1.214	-0.097	0.643	-0.046	-0.071	-0.083	0.571	0.128	1.357
DAD-03	0.787	-0.0018	0.540	-1.198	0.617	-0.282	0.034	-3.169	-0.651	-8.099	-0.587	-3.803	-0.123	-6.690	0.710	-1.479
DAD-04	0.528	-0.00138	0.411	1.326	0.175	0.698	0.316	1.256	-0.492	-2.791	0.120	0.419	-0.383	-2.512	0.263	0.907
DRA-04	0.821	-0.00088	0.075	0.951	0.008	0.211	0.183	1.638	-0.192	1.638	0.204	1.110	-0.022	2.061	-0.182	0.211
DRA-05	-0.251	0.00033	-0.083	-0.053	-0.103	-0.264	-0.178	-0.264	0.281	2.327	-0.077	-0.264	0.235	1.798	-0.158	0.000
ESU-18	0.588	-0.000009	0.633	2.169	0.273	1.024	0.137	0.964	-0.410	-0.121	0.068	0.241	-0.194	0.060	0.126	1.567
FUR-07	0.085	0.000006	-0.040	-0.106	-0.009	-0.106	0.052	0.053	-0.043	-0.639	0.014	0.053	-0.017	-0.692	0.003	-0.319
FUR-08	0.891	-0.0147	0.102	0	0.141	0.263	0.056	-0.316	-0.196	-1.633	0.009	0.000	-0.084	-1.369	0.076	-0.421
TBE-05	0.783	0.01288	0.132	0.450	-0.166	-0.550	0.176	0.500	-0.010	-0.100	-0.141	-0.450	-0.066	-0.250	0.207	0.500
TON-01	0.660	-0.01148	0.098	-0.111	0.037	-0.167	-0.053	-1.166	0.016	-2.166	-0.125	-1.111	0.001	-1.111	0.124	-1.222
TON-08	0.461	-0.01443	0.031	-0.112	0.015	-0.112	0.198	0.562	-0.214	-1.574	0.009	-0.056	0.105	-0.112	-0.114	-1.068
All Plots	**0.387**	-0.00024	**0.108**	**0.420**	0.028	0.010	**0.113**	0.577	**-0.141**	-0.563	-0.035	-0.209	-0.021	-0.077	0.055	0.241
Lower CI	**0.203**	-0.00062	**0.031**	**0.048**	-0.044	-0.144	**0.038**	-0.140	**-0.247**	-1.754	-0.123	-0.750	-0.096	-1.181	-0.039	-0.240
Upper CI	**0.565**	0.00017	**0.197**	**0.783**	0.118	0.185	**0.189**	1.237	**-0.045**	0.374	0.033	0.184	0.051	0.801	0.170	0.749

Table A2. Plot level trait changes based on biomass. All values are annual rates of change. For categorical variables Rel. = change in percentage of trees of that trait (percentage point yr^{-1}) and Abs. = change in biomass (Mg ha^{-1} yr^{-1}) of trees with that trait. Bootstrapped mean weighted by plot size and 95% CI are given for each trait. Significant changes across all plots are in bold.

Plot	Habitat Score (units yr^{-1})	Wood Density (g cm^{-3} yr^{-1})	Deciduous		Pioneers		NPLD		Shade Bearer		Understorey		Sub-canopy		Canopy	
			Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.	Abs.
ASN-02	0.599	-0.00086	-0.302	-235.7	-0.238	-252.3	0.027	311.5	0.211	805.9	0.008	17.1	-0.067	30.5	0.059	817.1
ASN-04	0.218	-0.00043	0.124	1395.9	0.161	1043.4	-0.124	415.7	-0.036	366.9	-0.005	63.6	-0.165	-62.0	0.170	1778.3
BBR-14	-0.198	0.00136	-0.113	125.0	-0.464	-1128.7	0.340	1218.1	0.124	698.0	0.025	83.4	0.013	140.5	-0.038	552.9
BBR-16	0.804	-0.00115	0.387	2970.5	0.167	1184.4	0.492	2374.3	-0.659	148.2	-0.074	-63.1	-0.277	-196.6	0.351	3901.7
BBR-17	0.709	0.00083	-0.020	149.2	-0.597	-1891.6	0.483	1684.6	0.114	507.4	-0.004	-11.2	-0.047	-141.6	0.052	448.7
BOR-05	0.825	-0.000009	0.164	1308.5	0.037	330.0	0.266	2170.6	-0.303	417.4	0.004	63.1	-0.295	476.0	0.291	2620.9
BOR-06	1.021	0.00008	0.100	592.8	0.096	322.2	-0.118	323.7	0.022	510.7	0.034	96.3	0.088	805.7	-0.122	300.4
CAP-09	-0.014	0.00012	0.035	403.6	-0.006	9.2	0.088	1129.0	-0.082	3370.4	-0.016	-52.2	-0.237	1473.3	0.253	2817.3
CAP-10	-1.647	0.00264	0.098	1567.7	-0.540	-584.3	0.570	3307.5	-0.031	1046.1	-0.414	-603.0	-0.074	800.4	0.488	3721.1
DAD-03	2.078	-0.00171	0.527	276.0	0.480	502.2	0.179	-134.9	-0.658	-1017.9	-0.199	-337.1	-0.496	-1039.8	0.696	286.4
DAD-04	0.543	0.00028	0.472	2359.5	0.232	1580.1	0.131	1075.4	-0.362	-642.1	0.004	139.7	-0.343	-568.6	0.339	2381.4
DRA-04	0.503	-0.00078	-0.168	-248.5	-0.371	-936.0	0.667	1996.5	-0.296	-1311.3	0.037	112.5	-0.141	-921.6	0.105	636.6
DRA-05	0.104	-0.00023	-0.128	574.2	-0.277	-123.3	0.011	646.2	0.265	1240.3	-0.015	-16.8	0.164	1048.1	-0.149	706.0
ESU-18	1.010	0.00021	0.633	1138.0	0.128	248.8	0.267	781.5	-0.395	334.1	0.019	32.2	-0.378	-142.0	0.359	1497.7
FUR-07	-0.066	0.00008	0.024	849.7	-0.098	144.0	0.316	1829.6	-0.219	769.1	0.012	92.9	-0.154	909.8	0.143	1627.7
FUR-08	-0.101	-0.00006	-0.109	187.9	-0.140	-23.2	0.199	808.1	-0.059	215.4	0.006	25.4	-0.221	62.3	0.215	910.6
TBE-05	0.696	-0.00014	0.317	1822.5	0.055	707.5	0.035	1214.1	-0.090	694.9	-0.055	-57.7	-0.243	-92.4	0.298	2747.7
TON-01	0.455	-0.00026	0.169	809.7	-0.030	-69.1	-0.119	-357.9	0.149	848.3	-0.017	-59.6	-0.035	-74.3	0.053	487.1
TON-08	0.751	-0.0014	0.131	586.7	0.099	466.4	0.133	662.6	-0.231	-399.8	0.019	72.4	-0.122	-220.9	0.104	902.0
All Plots	**0.429**	-0.000069	**0.120**	**888.7**	-0.069	73.9	**0.206**	**1158.8**	**-0.138**	449.2	-0.037	-25.7	**-0.153**	137.3	**0.190**	**1535.2**
Lower CI	**0.067**	-0.00051	**0.025**	**532.2**	-0.207	-319.2	**0.100**	**722.3**	**-0.262**	-4.39	-0.094	-122.5	**-0.230**	-174.3	**0.095**	**1024.7**
Upper CI	**0.770**	0.00043	**0.223**	**1284.7**	0.060	453.4	**0.318**	**1600.8**	**-0.022**	952.7	0.005	47.8	**-0.079**	467.1	**0.290**	**2081.9**