Eco-Hydrology of a Seasonally Dry Tropical Forest

Tree Growth, Belowground Water Dynamics and Drought-Vulnerability

Rutuja Chitra-Tarak

Thesis

Submitted for 'Doctor of Philosophy' in the Faculty of Science,
Centre for Ecological Sciences, Indian Institute of Science, Bangalore.

Declaration

I, hereby, declare that the work reported in this thesis has been carried out by me in the Centre for Ecological Sciences, Indian Institute of Science, under the supervision of Prof. R. Sukumar. I also declare that this work has not formed the basis for the award of any degree, diploma, fellowship, associateship or similar title of any university or institution.

Rutuja Chitra-Tarak
Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560012, India.

April 2016, Bangalore.

Dedicated to my parents,

Chitra and Tarak,

And brother, Anubandh.

Table of Contents

Acknowledgements

This thesis would not have been possible without the support of a number of individuals and agencies. I am thankful to them all:

Raman Sukumar, who gave me the freedom to do whatever I wanted to do and provided all the support that helped me develop a strong and autonomous research program.

Nagesh Kumar whose support and kindness I am deeply indebted to.

Laurent Ruiz, for spending countless hours in the last couple of years brainstorming, mentoring and teaching me hands-on science practice, all of which helped me blossom as a researcher. I thoroughly enjoyed walking through the uncharted terrains of eco-hydrology and co-creating with him.

Milind Watve, for introducing me to the world of evolutionary ecology during my undergrad years, fascination of which remained the driving force that kept me at PhD.

Sandeep Pulla, Geetha Ramaswami, Nandita Mondal, Karpagam Chelliah, who were my sounding boards over the years, and such fun at that, be it in the field or lab. Meera, Meghna for all their love and care, especially during long-stays in Mudumalai field station. My other talented lab-mates whose warmth has been pervasive: Ratna Ghosal, Shalu Kumar, Soumya Prasad, Rajiv, Ankur Shringi, Ekta Chaudhary, Ishani, Ramyabala, Lokesh Naik, Rayees Mallik, Sanjeeta. Nirmala and Palani, for their efficient help with all smiles.

Dattaraja and Suresh, for helping me with plant identification in Mudumalai, for sustaining through decades of hard-earned forest dynamics plots data collection and accommodating yet another researcher in the resource crunch for field assistants, vehicles, drivers and diesel. Bharannaiah for being the support that he is at the Masinigudi field station. Manavalan for managing the accounts.

Field assistant Kunmari (Dumba) accompanied me for the largest period of field work. His self-learning abilities always made my eyes bright. A quick-learner, his botanical and arithmetic abilities ensured that I collected reliable data. Whoever has been with Kulbomma knows what a sheer delight he is to be with. Besides help with data collection, his presence on field trips ensured that I was well-cared for. Chinnabomma accompanied me in the early years of field work and ensured that I collect good data. Siddha, Raja, Pauli Mara, Krishna, Alu, Banta, Keta, Mohan, Madan, Mandba and all the field assistants who helped in some way or the other and made sure that I was safe in field. Cook Mara for serving delicious southern Indian food I would always look forward to. Raghavendra, V. Bala, Shravan Kumar, Nachiketha, Patagar, Prakash, Veeresh, Nanja, Shuta and Vivek for their resourceful company.

Ayesha Prasad for the travels in her Jeep in Mudumalai, for long chats and friendship. Ramdas and Rama for happy welcomes at their coffee estate in Thorapalli, for rain-guage data and friendship.

Field Directors and all the Range officers of the Mudumalai National Park, DFOs of Bandipur National Park and Rangers of the Mulehole range for their support of our forest studies.

The highly talented and self-motivated peers of CES, some of whom I had a better chance of spending time with, or just having them around: Shreekant, Joy, Hari, Sandhya, Sneha, Vijay, Jahnavi, Alok, Natasha, Vivek, Mahua, Ashok, Ranjana, Monisha, Diptarup, Rittik, Samira, Paromita, Souvik, Anindita Brahma, Vignesh, Lakshy, Navendu, Nikita, Suman, Jayabharathy, Anne, Bharti, Priti, Harish, Ishan, Roy, Viraj, Varun, Aparna, Rohini, Murali, Karthick B. Friends from the larger ecology community: Anagh Purandare, Amit Kurien, Aniruddha Marathe, Vidyadhar Atkore, Rohit Naniwadekar, Chandrima Home, Raman Kumar, Nibedita Mukherjee, Sartaj Ghuman, Robin, Nandini, Gowri.

CES faculty, for being inspiring teachers, for building such a thriving community of researchers around, and fostering an atmosphere of greater autonomy for students. Former chairperson, Raman Sukumar, and current chairperson of the Centre for Ecological Science, Renee Borges, for support throughout my PhD.

Kavita Isvaran, Vidyanand Nanjundiah, NV Joshi, Venu Vuruputur, Debasis Sengupta, Venu Madhav Govindu, Suhel Quader for conversations and support.

All the staff at CES for swiftly handling paperwork, especially Raghavendra Rao, Basavaraj, Laxmi, Madhu, Murugeshachar. The efficient and welcoming staff of CES library: Venkatesulu, Reva Rani and librarian Yashvant Kanade.

Jean Riotte for the supportive force that he has always been. Matthieu Cisel for being a sounding board during early years of my PhD, accompanying me on several field missions and lab works; for his friendship. Several other people at the vibrant Indo-French Cell for Water Sciences (IFCWS)—a mixed international lab by IRD & IISc that was has been my other home—especially, Jean-Jacques Braun, Sekhar Muddu, M. S. Mohan Kumar, S. Subramanian, Pascal Jouquet, Jean-Louis Duprey, Fabien Durand, Fabrice Papa, Bhuvaneshwari, Praveen Kumar, Hemanth Moger, Kumar C., Venu, Shanmugam Mani, Amit Kumar. Several visitors over the years: Aurelie Dupard, Meyssoun Kabbaj, Maud Bonzi, Maël Ameline, Anne Pando, Melanie, Tom Lecomte, Yulie Campagna, Eloïse Renault Allard, Fanny Guinness, Etienne Aibola, Shanto Shahin.

My collaborator, Sean McMahon, for advice and friendship. Several fantastic researchers with the Smithsonian Centre for Tropical Forest Science-ForestGEO network for conversations at workshops.

Naveen Gandhi and Hemant Borgaonkar for help with a batch of tree-rings analyses at IITM, Pune.

Administration of CSIR for granting and managing my Junior and Senior Research Fellowships. French Embassy in India and the Govt. of India for granting me Cellular-Mix-CEFIRSE Fellowship. Stéphane Audry of JET/LMTG, Tolouse, and Dominique Genty and Valerie Doux of LSCE, Paris for hosting me on this grant. Ministry of Environment and Forest for continued financial support for the long-term forest dynamics research in the Mudumalai National Park. The Indo-French Cell for Water Sciences (IFCWS, IISc) for supporting me with a Research Associateship.

Friends at Concern, IISc: Ashok Krishnan, Jishnu Sadashivan, Roobala Chelladurai, Soundarya Iyer, Kaushik Senthoor, Anirban Mitra, Kishor Govinda, Manuj Mukherjee, Prathamesh Taruga and Subhankar Chakraborty.

Subhankar and Femi for all the chai-coffee breaks and friendship. Subhankar with who I got involved with organizing several events though Concern, BGVS and ESS. Those two and Paromita Verma, Anuradha Kumar, Ekta Chaudhary and several others for their comradeship, especially during our agitation to lift restriction on men's entry in women's hostel. That restriction is still there, unfortunately, waiting for women and men's wish and will to question the status quo.

Many a friends on campus, Amit Verma, Adway Mitra, Anirban Mitra, Gaurav Mendiratta for brightening campus life and comradeship. Geetanjali and Ramanpreet for their live and loving company as neighbors in the hostel.

Aniruddha Abhyankar, for several years of fun and warm journey together, and for all the support for my journey ahead alone.

Prema Iyer, for arranging accommodating in the first few months of our stay in Bangalore, when we badly needed it. Our lovely house-owners Divakaran and Komala for their warmth, and renting us their fresh house. Rimpa and Sumo for their fun company.

My Parents—Chitra and Tarak, for sowing the seeds, and then letting me be. My brother, Anubandh, for always being there. Ranjana Pathak for love and friendship. Pranita, for her loving care.

Arvind Lodaya, for meeting me at some transformative times, and bringing along my natural habitat where I could blossom as a tree. For being the natural mentor that he is. For love and solace.

Finally, the forests and the forest-dwelling communities, for being there, and being such a solace.

I am sure I would have forgotten to mention many that helped my journey during this PhD and I will remember them soon after this goes to print! I am grateful to you all.

Synopsis

Tropical forests are storehouses of more than half of the world's biodiversity and play a key role in global carbon, water and energy cycles. However, as a consequence of rapid anthropogenic climate change, biodiversity and climate functions of these forests are under a threat. Climate is changing not only in mean state but its variability is increasing, with extreme events such as droughts, heat waves and storms also rising. Water is fundamental to plants' existence, and in the tropics, is a key determinant of plant species' richness, composition, growth and survival. There is thus an increasing interest in understanding how changing rainfall may cause functional changes in forests or change their species composition. Therefore, **the overarching goal of this dissertation was to understand the impact of water variability on tropical forest tree growth and vulnerability to drought.**

Forest tree growth along spatial and temporal rainfall gradients

Observational studies that measure whole forest tree growth along spatial or temporal gradients of rainfall are the most common way of formulating forest growth response curves to water availability, when manipulative experiments are cost-prohibitive or impractical (fire or large mammal disturbance). In the tropics, since very few species show anatomically distinct tree rings, estimating tree growth from trunk diameter is the standard practice to obtain growth patterns across species. However, this method—of equating woody growth to diameter change--is susceptible to bias from water-induced stem flexing. In the absence of bias correction, temporal variability in growth is likely to be overestimated and incorrectly attributed to fluctuations in resource availability, especially in forests with high seasonal and inter-annual variability in water. This problem has been largely ignored in the absence of any corrective measure and due to under-appreciation of the magnitude of error. While diameter re-censuses in permanent sampling plots (PSPs) have been most commonly done at 3-5 year scale (using a graduate tape), increasingly they are done at seasonal and annual scales (using band dendrometers) to closely match variation in rainfall, the scales at which hydrostatic bias may be greater in magnitude relative to woody growth. Besides, along a spatial rainfall gradient, inter-annual variability in water may vary, causing systematic differences in the hydrostatic bias for forests along the gradient. Therefore, **one broad objective of this thesis was to evaluate the problem of hydrostatic bias in whole forest growth-rainfall relationship at annual and supra-annual scales, for temporal as well as spatial rainfall gradients and propose and test a novel corrective solution.** Further, it also examines if growth-diameter relationship vary along the spatial gradient, which it may arise due to differences in light environments and/or disturbance history and species composition.

The missing link of Eco-hydrology

Differential responses of tree species in terms of growth and survival to variation in water that they can access, the proximate cause—is likely shaped through their life-history strategies, the ultimate cause. However, we neither know the depths at which the diverse tree species in a forest draw water from and its dynamics, nor variation in water at those depths vis-à-vis rainfall patterns—for lack of appropriate methods. This has been a key missing link in understanding how water shapes trees' life-history strategies, their demographic trade-offs and co-existence, and also our predictive ability to determine species-specific responses to changing rainfall patterns, especially droughts. Since droughts are highly stochastic events and trees' responses to their drought "experiences" may be revealed at decadal scales, long-term evaluations are key. Therefore, **the second broad objective of this thesis was to develop a framework to determine trees' water uptake depths, variation in water availability at those depths and trees' demographic responses over multiple decades. From this, to understand how belowground hydrology shapes drought-vulnerability, demographic trade-offs and coexistence of forest tree species.**

This thesis titled—**Eco-Hydrology of a Seasonally Dry Tropical Forest: Tree Growth, Belowground Water Dynamics and Drought-Vulnerability**—is organized as follows: Chapter 1 lays down an introduction to the thesis, followed by a description of the study site and datasets used in the thesis in Chapter 2. This thesis uses a variety of methods and multiple datasets, all of which are from the protected Seasonally Dry Tropical Forests of the Western Ghats in southern India in the Mudumalai and Bandipur National Parks. It is then followed by three data chapters:

Chapter 3 describes the seasonal fluctuations in a five year long (1980-1985) tree diameter time series (using dendrometers) of a Seasonally Dry Tropical Forest in Bandipur National Park to illustrate the issue of hydrostatic stem-flexing. It investigates the possibility that band dendrometers may themselves underestimate stem shrinkage at diurnal or seasonal scale. It also evaluates if there could be a best season and time of the day for undertaking forest diameter censuses that can minimize hydrostatic bias.

Chapter 4 *(published in Forest Ecology and Management)* measures the hydrostatic bias in a sample of trees in a 50 ha PSP of a Seasonally Dry Tropical Forest in Mudumalai National Park, and proposes a novel way to correct this bias at the whole community level in the 20 year long 4-year interval growth time series.

Chapter 5 (*in review with Environmental Research Letters*) investigates and presents two new confounding factors in growth-rainfall relationships along a spatial rainfall gradient: hydrostatic bias and size-dependency in growth rates. For this it evaluates forest tree growth estimates in seven 1-ha PSPs (~800 trees, 3-year annual time series using dendrometers) along a 1000 mm rainfall gradient spanning a mesic savanna-moist forest transition in Mudumalai National Park. Using the period for which seasonal diameter time series was available (2 yrs), it evaluates if the extent of seasonal fluctuations systematically vary along the gradient—most likely due to hydrostatic stem flexing. It also describes the presence of an anomalous size-diameter relationship in the mesic savanna from a large plots (50 ha PSP, diameter records using graduated tape). These observations are then used to draw insights for "space for time" substitution modeling.

Chapter 6 (*in prep for Nature Plants*) analyses belowground water environments of trees over two decades (1992-2012), a period that includes a prolonged and intense drought, in the 50 ha PSP of a Seasonally Dry Tropical Forest in Mudumalai. It uses a locally parametarised dynamic hydrological model in which site rainfall is also a forcing variable. It then develops a novel dynamic growth model and inversely estimates water uptake depths for adult trees of all common species (include ~9000 trees) in the PSP from their above-ground growth patterns over two decades vis-à-vis belowground water availability at multiple depths. It then examines if species' water uptake depth obtained thus is a predictor of their drought-driven mortality. Finally, this is used to evaluate the hydrological niche partitioning tree species operate under and how that drives their water uptake strategies, demographic trade-offs, and drought-vulnerability.

Chapter 7 summarises the thesis and suggests future directions.

Publications

Chitra-Tarak, R., Ruiz, L., Pulla, S., Dattaraja, H.S., Suresh, H.S., Sukumar, R., 2015. And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations. *Forest Ecology and Management.* 336, 129–136.

Chitra-Tarak, R., Ruiz, L., McMahon, S. M., Dattaraja, H.S., Mohan Kumar, M.S., Suresh, H.S., Riotte, J., Sukumar, R., Multi-scale precipitation patterns drive belowground niche partitioning and drought effects in a seasonally dry tropical forest. *In prep for Nature Plants*.

Chitra-Tarak, R., Dattaraja, H.S., Suresh, H.S., Sukumar, R. Hydrostatic bias in measuring forest tree growth changes along a tropical precipitation gradient—implications for forest growth–climate relationships. *In review* with *Environmental Research Letters.*

Author Contributions

All chapters presented in this thesis were written by Rutuja Chitra-Tarak under the guidance of Prof. Raman Sukumar. Specific author contributions to data chapters are detailed below:

Chapter 3: The problem of hydrostatic stem-flexing in estimating tree growth and the timing of dendrometer censuses

Rutuja Chitra-Tarak, Raman Sukumar.

RCT designed the study, collected and analysed data and wrote the first draft of the chapter. RS provided guidance. RCT was the lead author of the chapter.

Chapter 4: And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations

Rutuja Chitra-Tarak, Laurent Ruiz, Sandeep Pulla, H. S. Dattaraja, H. S. Suresh, Raman Sukumar.

RCT and LR designed the study. RCT collected tree rings data. RS conceived, established and coordinated the Mudumalai 50ha Forest Dynamics Plot programme, DHS and SHS coordinated and collected field data. RCT analysed data and wrote the first draft of the paper. LR and RS provided guidance on analysis and writing. SP provided analytical inputs. All co-authors commented on the paper. RCT was the lead author on the paper.

Chapter 5: Hydrostatic bias and size-dependency in tree growth rates change along a precipitation gradient in a seasonally dry tropical forest

Rutuja Chitra-Tarak, H. S. Dattaraja, H. S. Suresh, Raman Sukumar.

RCT and RS designed the study. RCT collected tree rings data and Mudumalai 1-ha plot dendrometer data. RS conceived, established and coordinated the Mudumalai 50 ha and nineteen 1-ha Forest Dynamics Plot network, DHS and SHS coordinated and collected field data. RCT analysed data and wrote the first draft of the paper. RS provided guidance on analysis and writing. All co-authors commented on the paper. RCT was the lead author on the manuscript.

Chapter 6: Multi-scale precipitation patterns drive belowground niche partitioning and drought effects in a seasonally dry tropical forest

Rutuja Chitra-Tarak, Laurent Ruiz, Sean M. McMahon, H. S. Dattaraja, M.S.M. Kumar, Jean Riotte, H. S. Suresh, Raman Sukumar.

RCT and LR conceived and designed the study and carried out data analyses. RS conceived, established and coordinated the Mudumalai FDP programme, DHS and SHS coordinated and collected field data. LR conceived and established, LR, MSMK and JR coordinated Mulehole hydrological monitoring programme, LR and JR collected field data. RCT wrote the first draft of the manuscript. LR and SMM added inputs to the writing. SMM contributed to analytical tools used in the analyses. All co-authors commented on the manuscript. RCT was the lead author on the manuscript.

Chapter 1

General Introduction

Tropical forests under a changing climate

Tropical forests are storehouses of more than half of the world's biodiversity and play disproportionate role in the global carbon, water and energy cycles (IPCC 2001; Wright 2005). Forests help mitigate climate change in several ways. For example, they sequester carbon dioxide in their wood, locking it away for decades to centuries (Malhi, Meir & Brown 2002) and recycle belowground water back into the atmosphere via evapotranspiration, thereby reducing atmospheric temperature and availing moisture for re-precipitation (Milly & Dunne 1994; Kleidon & Heimann 1999; Ducharne & Laval 2000).

As a consequence of rapid anthropogenic climate change biodiversity and climate functions of these forests are under a threat (IPCC 2014). Climate is changing not only in mean state but its variability is increasing, with extreme events such as droughts, floods, heat waves, fires and storms expected to rise (IPCC 2013). These changes may cause functional changes in the extant forest or change their species composition. For example, rising CO_2 may act as a photosynthetic fertilizer causing tree growth to increase, while rising temperature may increase respiration and cause tissue damage. These extreme events may cause selective species die-off and thereby induce functional changes in the forest. In recent years, drought and heat-induced mortality of trees is found to be widespread across all vegetated continents (Allen *et al.* 2010; Hartmann *et al.* 2015). Forests are increasingly found to be changing in composition, structure and function (Phillips *et al.* 2010; Bennett *et al.* 2015), and whether they will continue to act as a sink of carbon or turn into a source has been an intense area of investigation in the last couple of decades (Phillips *et al.* 1998; Baker *et al.* 2004; Clark 2004; Doughty *et al.* 2015; Brienen *et al.* 2015). If we are to understand and predict responses of whole forests and individual species to climatic change, we need to evaluate their vulnerability to climatic stressors in terms of key plant fitness or performance measures such as growth and mortality.

Water as a key limiting factor for plant performance

As Silvertown, Araya & Gowing (2015) state succinctly:

"Terrestrial plants use water for just about every function imaginable. It is used structurally to provide cell turgor, as a raw material, a solvent, a transport medium and a coolant. Transpiration of water is the source of motive power in the xylem, and the photolysis of water provides hydrogen atoms for the biosynthetic reactions of photosynthesis. Plants also require a flux of water in order to take up nutrients."

Water availability is found to be the most important environmental factor within the tropics driving tree species richness (Gentry 1988; ter Steege *et al.* 2006), composition (Hall & Swaine 1976; Bongers, Poorter & Hawthorne 2004; Suresh *et al.* 2011), distribution (Swaine 1996; Bongers *et al.* 1999; Engelbrecht *et al.* 2007; Balvanera, Quijas & Pérez-Jiménez 2011), growth (Nath *et al.* 2006; Feeley *et al.* 2007; Toledo *et al.* 2011) and survival (Engelbrecht *et al.* 2006; McDowell *et al.* 2008; Allen *et al.* 2010). Species-specific responses in terms of performance to variation in water availability – including under the varied intensity and frequency of droughts – are needed to predict their fates under changing water environments.

Variability in water

Water availability is highly heterogenous in space and time: not only does water vary spatially across micro (1-100 m) and macro topographic (100 m-1 km) gradients and along rainfall gradients (1 km – 10/100 km); it also varies by vertical depth belowground. Interacting with the temporal dynamics of rainfall this can create great variety in water environments as variability in rainfall operates at multiple scales—seasonal and inter-annual to decadal scales. For example, in a dry forest top soil was found to be dry than deep soil, while in the wet season inverse was the case (Markesteijn *et al.* 2010). Although evaluation of plant-available water had largely been limited to soils, trees uptake water deep below the soil layer—from the weathered rock. The dynamics of water that operates in this zone – typically at supra-annual to decadal scales (Schwinning 2010; Ruiz *et al.* 2010; Schwinning & Kelly 2013) – is far underappreciated, let alone accounted for. Barring phreatophytes (Orellana *et al.* 2012), which uptake free water from the water table or the capillary fringe, most species uptake water from unsaturated zones of soil and weathered rock—the vadose zone.

Natural climatic gradients as tools to generate forest and species response curves

Experimental manipulation of adult tree water environment is an extremely costly undertaking unlike seedlings, thus examples of the former are sparse (but see, recent large-scale ecosystem experiments such as the Amazon Fertilisation Experiment: http://gtr.rcuk.ac.uk/projects?ref=NE/L007924/1), or is unmanageable under disturbance (fire or large mammals). Most studies on adult trees tend to be natural/observational experiments in which whole ecosystem (Marthews *et al.* 2012a) or individual plant performance (Rapp *et al.* 2012) is correlated with climatic conditions across sites (along a spatial rainfall gradient in the above examples), or with temporal variation in rainfall at a single site. In the absence of, or in addition to, long-term temporal observational studies, spatial environmental gradients are used as a "space for time" substitute to generate whole forest, or species-specific, response curves. However, as illustrated by Dunne et al. (2004), "The value of predictions from gradient analyses depends on the assumption that ecosystems will track changing climate over time in the same way that ecosystems now vary with climate variability over space. In general, long-term adaptation to local climatic conditions, fine-scale environmental heterogeneity, co-varying abiotic factors, non-monotonic changes, and differences in time constants may confound the straightforward use of spatial gradients to predict responses to global warming (Peters et al. 1991, Bazzaz and Wayne 1994, Villalba et al. 1994, Vitousek 1994)."

Drought tolerance

Currently mechanisms of drought mortality are so poorly understood that DGVMs (Dynamic Global Vegetation models) cannot predict drought-induced mortality of trees (Anderegg et al., 2013; Meir et al., 2015). Plants mechanisms for dealing with drought are largely classified into drought-avoidance and drought-tolerance (Poorter & Markesteijn 2008; Comita & Engelbrecht 2014). Drought-avoidance mechanisms prevent or delay species from experiencing low tissue water potentials: by continual water uptake via deep and/ or extended root systems, or water storage in stems, leaves or roots; or alternatively, by minimizing transpirational water loss (isohydry) via stomatal closure or leaf shedding (deciduousness). Drought-tolerance mechanisms allow plant to maintain water transport through their xylems even under conditions of low water availability and low plant water potentials (anisohydry) by mechanisms that maintain leaf turgor through high osmotic potentials or xylem structures that avoid cavitation failure.

Perhaps due to the difficulties involved in incorporating plants rooting depths and dynamic access to water, the current framework of species drought-vulnerability largely positions species on an axis of isohydry-aniosohydry (McDowell *et al.* 2008; Skelton, West & Dawson 2015). Isohydrous species are hypothesised to be vulnerable to prolonged drought through carbon starvation, while anisohydrous species are thought to be vulnerable to intense drought.

However, these strategies are not measured and evaluated against the drought "experienced" by species, and very rarely are these traits linked with plant performance (Comita & Engelbrecht 2009). How meteorological droughts translate into hydrological and ecological drought leading to physiological damage ultimately leading to their death is unknown, and urgently sought to be understood to equip our predictive abilities (Anderegg, Anderegg & Berry 2013).

Hydrological niche partitioning, functional trade-offs and plant responses

To predict plants responses under changing environment, can we draw insights from how plants have adapted to make a living in their environment? Niche theory predicts that each species specializes on its respective niche – a multiple resource environment that includes material, space, time as well as energy – and that this specialization allows them to coexist. This specialization is thought to operate through a specialized suit of physiological or morphological properties that species possess—the functional traits that drive their performance. Such specialization however entails that plants investments in their body structures and function to thrive under certain conditions would come at a cost of their performance under other conditions. Increasing evidence suggests that "trait trade-offs give rise to acquisitive species and conservative species. Acquisitive species are geared toward high resource acquisition rates and high growth and are successful in high resource habitats, whereas conservative species are geared toward high resource conservation, high stress tolerance, and high survival, and they are successful in low resource habitats." (Sterck *et al.* 2011)

Interestingly, despite the fundamental importance of water to plants, the first review paper on hydrological niches only occurred as recently as in 2015. In this review, Silvertown, Araya & Gowing (2015) argue that,

"Water is so obviously essential to physiological functions that it is arguable that ecologists have overlooked the more subtle importance of water to plant community structure, except in habitats where it is clearly in short supply. Part of the reason for this oversight must be that water, like light, O_2, CO_2 and the major nutrients N, P and K, is an essential resource for all plants and there just do not seem to be enough ways for species to partition these into the hundreds of niches required for stable coexistence in the most species rich plant communities (Silvertown 2004).**"**

Studies surveyed in this review, however, showed that Hydrological Niche Segregation (HNS) is widespread across arid to wet vegetation types, but the mechanisms and consequences of HNS were less clear. In arid communities temporal partitioning was found to promote coexistence through the storage effect—partitioning of recruitment opportunities among years caused by species specializing on particular patterns of temporal variance of water supply. This was yet to be found in other ecosystems. Majority of studies surveyed here were found to partition water as a resource, but very few of these studies had investigated trade-offs underlying the HNS. All of these observational studies used stable isotopes to compare different sources from which species drew water.

Schwinning & Kelly (2013) describe the multiple scales and ways by which water resource varies in time. However, compared to spatial niches, temporal niches have been much less explored and investigated. Even in water-limited systems presence of temporal niches is not widely accepted. At best, it is largely thought to be taking place in the plant regeneration phase with juveniles of co-existing species taking differential advantage of pulsed resources. Schwinning & Kelly (2013) state that "the most essential unresolved question is the extent to which community composition and dynamics are governed by the characteristics of juvenile or adult stages." They opine that discoveries have been limited by the demanding time scales – of decades-to-centuries – at which these phenomena should be observed.

The missing link of Eco-Hydrology

"Ecohydrology may be defined as the science which seeks to describe the hydrologic mechanisms that underlie ecologic patterns and processes." (Rodriguez-Iturbe 2000). As illustrated above, plant performance is typically measured against spatio-temporal variability in rainfall (Nath *et al.* 2006; Rapp *et al.* 2012), or that in soil moisture, but that mostly in 2-D space (Comita & Engelbrecht 2009), or against plants physiological and anatomical traits, which are hypothesised to confer them tolerance against droughts of different duration and intensity (McDowell *et al.* 2008; Skelton *et al.* 2015).

However, the key aspect that limits our power to predict plant response to water availability, or our understanding of the mechanisms and consequences of hydrological niche partitioning is the absence of measurement of plant performance against actual water availability. This is largely due to methodological limitation to measure plant's actual water availability over the time scales at which tree water environments are likely to vary—from seasonal to decadal scales. Exacerbating this challenge is the challenge of measuring trees water uptake depth, the vertical depths over which trees actually uptake water that can vary dynamically over time.

Hydrostatic stem flexing as a key bias in tree growth measurements

Besides being a resource for plant growth, water also appears to be interference in estimations of plant growth. In permanent sampling plots of forests, tree growth is estimated by measuring changes in tree diameter at the same height through time (Condit 1998). However, changes in diameter can arise not only due to growth increment, but also due to differences in tree water status at successive measurement occasions (Sheil 1995; Baker *et al.* 2002). Conditions under which large differences may occur in tree water status between census intervals, and where woody growth increment is relatively smaller, changes due to water-induced stem flexing can cause substantial bias in growth estimates. Permanent sampling plots are increasingly being used to serve as forest dynamics observatories around the world (Phillips *et al.* 1998; Anderson-Teixeira *et al.* 2015). In PSPs individual tree growth is typically monitored every few years using graduated tapes or calipers. In recent years it is being monitored with the use of dendrometer bands to more intensively track carbon stocks and fluxes on shorter time scales (Marthews *et al.* 2012b). At these scales hydrostatic bias may be of even larger magnitude relative to growth, yet it has been largely ignored (but see, Sheil 1995; Baker *et al.* 2002), its magnitude is rarely evaluated, and no method has been proposed so far for its correction.

Research Objectives

In this thesis, using PSPs in a seasonally dry tropical forest in the Western Ghats, India as a case study, my objective were to (i) evaluate extent of hydrostatic bias in forest tree growth estimates and propose a possible solution; (ii) analyse tree growth response along a spatial rainfall gradient and evaluate significant confounding variables; and (iii) estimate where do trees uptake water from, how hydrological niche partitioning operates for adult trees, and how does it shape species demography and drought-vulnerability.

Thesis outline and hypotheses tested

This thesis is organized as follows: Chapter 1 lays down an introduction to the thesis (this chapter), followed by a description of the study site and datasets used in the thesis in Chapter 2. It is then followed by four data chapters:

Chapter 3 describes the seasonal fluctuations in a historical five-year long dendrometer-based tree diameter time series from a Seasonally Dry Tropical Forest (SDTF) to illustrate the issue of hydrostatic stem-flexing. I evaluate the extent of seasonal tree stem shrinkage and expansion and test the hypothesis that the extent of hydrostatic bias can be a significant problem in estimating a time series of annual tree growth, especially when it is to be evaluated against variation in a resource or climatic conditions. I also test if hydrostatic bias can be avoided at supra-annual scale or by limiting diameter measurements to end-of-wet or dry season. Additionally I also tested if dendrometers can accurately track diurnal and seasonal diameter changes.

Chapter 4 measures the hydrostatic bias in a sample of trees in a 50 ha PSP, and proposes a novel way to correct this bias at the whole community level in the 20 year long 4-year interval growth time series. Comparing woody growth using tree rings and observed growth using a tape in a small number of trees in the 50 ha PSP, I tested whether significant biases in tree growth estimates were due to hydrostatic flexing. I then test whether biases in this small number of trees can be used as a proxy to correct biases in tree growth at the community level.

Chapter 5 evaluates forest tree growth estimates in PSPs along a rainfall gradient and investigates some significant confounding factors such as hydrostatic bias and size-dependent growth for "space for time" substitution modeling.

In this study, I evaluated key confounding factors in growth – precipitation gradient analysis using dendrometer based annual growth estimates of trees in permanent sampling plots (PSPs) along a distinct precipitation gradient in southern India. I evaluated tree growth relationships along this spatial precipitation gradient spanning a tropical dry deciduous forest to moist deciduous forest transition, and specifically examined if and how tree growth estimates along this gradient were influenced by (i) shift in the extent of stem hydrostatic bias, (ii) shift in growth – diameter allometric relationship, and (iii) species turnover along the gradient. Seasonal fluctuations in dendrometer based diameter time series was used to evaluate likely shift in hydrostatic bias. I adapted a novel method described in Chapter 4 that uses stem hydrostatic bias measured in a few trees at the center of this gradient and examined whether this could be used to estimate and correct for bias in annual diameter growth records of PSPs across the spatial precipitation gradient measured over three successive years. I also investigated growth-diameter relationship and shift therein along the rainfall gradient using dendrometer-based diameter census datasets at seven 1-ha PSPs. I also made use of the larger tape-based diameter census dataset from the 50-ha PSP situated at the center of the rainfall gradient to more closely examine this relationship for a tropical dry deciduous forest/mesic savanna.

Chapter 6 analyses belowground water environments of trees over several decades and proposes a novel way to measure effective uptake depth for adult trees of all common species in a 50 ha PSP. It evaluates the hydrological niche partitioning they operate under and how that drives species demography, especially drought-vulnerability, and demographic trade-offs at play. Here, I specifically tested the hypothesis that multi-scale dynamics of belowground water and trees differential uptake depths may result into their hydrological niche partitioning, which should reflects into their differential growth and mortality response to rainfall variation. The dynamics of belowground water—across the full depths at which trees likely uptake water—was examined over two decades using a locally calibrated and validated hydrological model. This combined with species variation in growth over this period was in fact used to inversely infer species water uptake depth dynamics by building a new dynamic model of water-stress on growth. While trees with deep water uptake are assumed to be buffered in a drought with deep water availability taken for granted, I tested whether this holds true for an extensive drought in a dry forest. I expected that if deep water is slowly exhausted in a prolonged drought and slowly replenished, this might result into greater water availability near the surface than at depth; and making species with deep water uptake are more vulnerable in such a drought. To test whether shallow or deep water uptake species died more in the excessive drought, the uptake depth rankings inferred inversely by the above method were then examined against species rankings for excess mortality under drought.

Chapter 7 summarises the thesis and suggests future directions.

References

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, 259, 660–684.

Anderegg, L.D.L., Anderegg, W.R.L. & Berry, J.A. (2013) Not all droughts are created equal: translating meteorological drought into woody plant mortality. Tree Physiology, 33, 672–683.

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer, J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S., Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M., Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J., Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K., Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena, D.M., Makana, J.-R., Malhi, Y., Marthews, T., Mat Serudin, R., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., de Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips, R.P., Sack, L., Sainge, M.N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J., Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S. & Zimmerman, J. (2015) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Global Change Biology, 21, 528–549.

Baker, T.R., Affum-Baffoe, K., Burslem, D.F.R.P. & Swaine, M.D. (2002) Phenological differences in tree water use and the timing of tropical forest inventories: conclusions from patterns of dry season diameter change. Forest Ecology and Management, 171, 261 – 274.

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., Vargas, P.N., Pitman, N.C.A., Silva, J.N.M. & Martínez, R.V. (2004) Increasing biomass in Amazonian forest plots. Philosophical Transactions of the Royal Society B: Biological Sciences, 359, 353–365.

Balvanera, P., Quijas, S. & Pérez-Jiménez, A. (2011) Distribution Patterns of Tropical Dry Forest Trees Along a Mesoscale Water Availability Gradient. Biotropica, 43, 414–422.

Bazzaz, F.A. & Wayne, P.M. (1994) Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. Exploitation of environmental heterogeneity by plants: ecophysiological processes above-and belowground. (eds M. Caldwell & R. Pearcy), pp. 349–390. Academic Press, San Diego, California, USA.

Bennett, A.C., McDowell, N.G., Allen, C.D. & Anderson-Teixeira, K.J. (2015) Larger trees suffer most during drought in forests worldwide. Nature Plants, 1.

Bongers, F., Poorter, L. & Hawthorne, W.D. (2004) The forests of Upper Guinea: Gradients in large species composition. Biodiversity of West African forests. An ecological atlas of woody plant species (eds L. Poorter, F. Bongers, F.N. Kouame & W.D. Hawthorne), pp. 41–52. CABI Publishing, Oxford, UK.

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. Journal of Vegetation Science, 10, 371–382.

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S.L., Vásquez Martinez, R., Alexiades, M., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragão, L.E.O.C., Araujo-Murakami, A., Arets, E.J.M.M., Arroyo, L., C, G.A.A., Bánki, O.S., Baraloto, C., Barroso, J., Bonal, D., Boot, R.G.A., Camargo, J.L.C., Castilho, C.V., Chama, V., Chao, K.J., Chave, J., Comiskey, J.A., Cornejo Valverde, F., da Costa, L., de Oliveira, E.A., Di Fiore, A., Erwin, T.L., Fauset, S., Forsthofer, M., Galbraith, D.R., Grahame, E.S., Groot, N., Hérault, B., Higuchi, N., Honorio Coronado, E.N., Keeling, H., Killeen, T.J., Laurance, W.F., Laurance, S., Licona, J., Magnussen, W.E., Marimon, B.S., Marimon-Junior, B.H., Mendoza, C., Neill, D.A., Nogueira, E.M., Núñez, P., Pallqui Camacho, N.C., Parada, A., Pardo-Molina, G., Peacock, J., Peña-Claros, M., Pickavance, G.C., Pitman, N.C.A., Poorter, L., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Restrepo, Z., Roopsind, A., Rudas, A., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Stropp, J., Talbot, J., ter Steege, H., Teran-Aguilar, J., Terborgh, J., Thomas-Caesar, R., Toledo, M., Torello-Raventos, M., Umetsu, R.K., van der Heijden, G.M.F., van der Hout, P., Guimarães Vieira, I.C., Vieira, S.A., Vilanova, E., Vos, V.A. & Zagt, R.J. (2015) Long-term decline of the Amazon carbon sink. Nature, 519, 344–348.

Clark, D.A. (2004) Sources or Sinks? The Responses of Tropical Forests to Current and Future Climate and Atmospheric Composition. Philosophical Transactions: Biological Sciences, 359, 477–491.

Comita, L. & Engelbrecht, B. (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. ECOLOGY, 90, 2755–2765.

Comita, L.S. & Engelbrecht, B.M.J. (2014) Drought as a driver of tropical tree species regeneration dynamics and distribution patterns. Forests and Global Change, Ecological Reviews (eds D.A. Coomes, D.F.R.P. Burslem & W.D. Simonson) Cambridge University Press.

Condit, R. (1998) Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer-Verlag, Berlin.

Doughty, C.E., Metcalfe, D.B., Girardin, C.A.J., Amézquita, F.F., Cabrera, D.G., Huasco, W.H., Silva-Espejo, J.E., Araujo-Murakami, A., da Costa, M.C., Rocha, W. & others. (2015) Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature, 519, 78–82.

Ducharne, A. & Laval, K. (2000) Influence of the realistic description of soil water-holding capacity on the global water cycle in a GCM. Journal of Climate, 13, 4393–4413.

Dunne, J.A., Saleska, S.R., Fischer, M.L. & Harte, J. (2004) Integrating experimental and gradient methods in ecological climate change research. Ecology, 85, 904–916.

Engelbrecht, B., Comita, L., Condit, R., Kursar, T., Tyree, M., Turner, B. & Hubbell, S. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. NATURE, 447, 80–U2.

Engelbrecht, B.M.J., Dalling, J.W., Pearson, T.R.H., Wolf, R.L., Gálvez, D.A., Koehler, T., Tyree, M.T. & Kursar, T.A. (2006) Short dry spells in the wet season increase mortality of tropical pioneer seedlings. Oecologia, 148, 258–269.

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

Gentry, A.H. (1988) Changes in Plant Community Diversity and Floristic Composition on Environmental and Geographical Gradients. Annals of the Missouri Botanical Garden, 75, 1–34.

Hall, J.B. & Swaine, M.D. (1976) Classification and Ecology of Closed-Canopy Forest in Ghana. Journal of Ecology, 64, 913–951.

Hartmann, H., Adams, H.D., Anderegg, W.R.L., Jansen, S. & Zeppel, M.J.B. (2015) Research frontiers in drought-induced tree mortality: crossing scales and disciplines. New Phytologist, 205, 965–969.

IPCC. (2001) Climate Change 2001:Impacts, Adaptation and Vulnerability. WMO/UNEP Intergovernmental Panel on Climate Change, Third Assessment Report.

IPCC. (2013) Climate Change 2013: The Physical Science Basis. (eds Stocker et Al.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

IPCC. (2014) Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Kleidon, A. & Heimann, M. (1999) Deep-rooted vegetation, Amazonian deforestation, and climate: results from a modelling study. Global Ecology and Biogeography, 8, 397–405.

Malhi, Y., Meir, P. & Brown, S. (2002) Forests, Carbon and Global Climate. Philosophical Transactions of the Royal Society of London. Series A: Mathematical, Physical and Engineering Sciences, 360, 1567–1591.

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

Marthews, T.R., Malhi, Y., Girardin, C.A.J., Silva Espejo, J.E., Aragão, L.E.O.C., Metcalfe, D.B., Rapp, J.M., Mercado, L.M., Fisher, R.A., Galbraith, D.R., Fisher, J.B., Salinas-Revilla, N., Friend, A.D., Restrepo-Coupe, N. & Williams, R.J. (2012a) Simulating forest productivity along a neotropical elevational transect: temperature variation and carbon use efficiency. Global Change Biology, 18, 2882–2898.

Marthews, T.R., Metcalfe, D.J., Malhi, Y., Huaraca, H.W., Riutta, T., Ruiz-Jaen, M., Girardin, C.A.J., Butt, N., Cain, R., Oliveras, M.I. & and colleagues from the RAINFOR and GEM networks. (2012b) Measuring Tropical Forest Carbon Allocation and C Ycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v2.2). Manual.

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

Meir, P., Mencuccini, M. & Dewar, R.C. (2015) Drought-related tree mortality: addressing the gaps in understanding and prediction. New Phytologist, 207, 28–33.

Milly, P.C.D. & Dunne, K.A. (1994) Sensitivity of the global water cycle to the water-holding capacity of land. Journal of Climate, 7, 506–526.

Nath, C.D., Dattaraja, H.S., Suresh, H.S., Joshi, N.V. & Sukumar, R. (2006) Patterns of tree growth in relation to environmental variability in the tropical dry deciduous forest at Mudumalai, southern India. Journal of Biosciences, 31, 651–669.

Orellana, F., Verma, P., Loheide, S.P. & Daly, E. (2012) Monitoring and modeling water-vegetation interactions in groundwater-dependent ecosystems. Reviews of Geophysics, 50, RG3003.

Peters, R.H., Armesto, J.J., Boeken, B., Cole, J.J., Driscoll, C.T., Duarte, C.M., Frost, T.M., Grime, J.P., Kolasa, J., Prepas, E. & Sprules, W.G. (1991) On the relevance of comparative ecology to the larger field of ecology. Comparative anaylses of ecosystems (eds J.J. Cole, G. Lovett & S. Findlay), pp. 46–63. Springer-Verlag, New York, New York, USA.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, Á.C.A., Chao, K.-J., Cardozo, N.D., 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, A., Vargas, P.N., Patiño, S., Peh, K.S.-H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J.W., Sonké, B., Thomas, A.S., Stropp, J., Taplin, J.R.D., Vásquez, R. & Vilanova, E. (2010) Drought–mortality relationships for tropical forests. New Phytologist, 187, 631–646.

Phillips, Malhi, Higuchi, Laurance, Nunez, Vasquez, Laurance, Ferreira, Stern, Brown & Grace. (1998) Changes in the carbon balance of tropical forests: evidence from long-term plots. Science (New York, N.Y.), 282, 439–442.

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

Rapp, J.M., Silman, M.R., Clark, J.S., Girardin, C.A.J., Galiano, D. & Tito, R. (2012) Intra- and inter-specific tree growth across a long altitudinal gradient in the Peruvian Andes. Ecology.

Rodriguez-Iturbe, I. (2000) Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamies. Water Resources Research, 36, 3–9.

Ruiz, L., Varma, M.R.R., Kumar, M.S.M., Sekhar, M., Maréchal, J.-C., Descloitres, M., Riotte, J., Kumar, S., Kumar, C. & Braun, J.-J. (2010) Water balance modelling in a tropical watershed under deciduous forest (Mule Hole, India): Regolith matric storage buffers the groundwater recharge process. Journal of Hydrology, 380, 460–472.

Schwinning, S. (2010) The ecohydrology of roots in rocks. Ecohydrology, 3, 238–245.

Schwinning, S. & Kelly, C.K. (2013) Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. Functional Ecology, 27, 886–897.

Sheil, D. (1995) A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. Forest Ecology and Management, 77, 11 – 34.

Silvertown, J., Araya, Y. & Gowing, D. (2015) Hydrological niches in terrestrial plant communities: a review. Journal of Ecology, 103, 93–108.

Skelton, R.P., West, A.G. & Dawson, T.E. (2015) Predicting plant vulnerability to drought in biodiverse regions using functional traits. Proceedings of the National Academy of Sciences, 112, 5744–5749.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vásquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. Nature, 443, 444–447.

Sterck, F., Markesteijn, L., Schieving, F. & Poorter, L. (2011) Functional traits determine trade-offs and niches in a tropical forest community. Proceedings of the National Academy of Sciences, 108, 20627–20632.

Suresh, H.S., Dattaraja, H.S., Mondal, N. & Sukumar, R. (2011) Seasonally Dry Tropical Forests in Southern India: An Analysis of Floristic Composition, Structure, and Dynamics in Mudumalai Wildlife Sanctuary. The ecology and conservation of seasonally dry forests in Asia (eds W.J. McShea, S.J. Davies & N. Bhumakphan) Smithsonian Institution Scholarly Press, Washington, D.C.

Swaine, M.D. (1996) Rainfall and Soil Fertility as Factors Limiting Forest Species Distributions in Ghana. Journal of Ecology, 84, 419–428.

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P. & Bongers, F. (2011) Climate is a stronger driver of tree and forest growth rates than soil and disturbance. Journal of Ecology, 99, 254–264.

Villalba, R., Veblen, T.T. & Ogden, J. (1994) Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology, 1450–1462.

Vitousek, P.M. (1994) Factors controlling ecosystem structure and function. Factors of Soil Formation: A Fiftieth Anniversary Retrospective (eds R. Amundson, J. Harden & M. Singer), pp. 87–97. Soil Science Society of America, Madison, Wisconsin, USA.

Wright, S.J. (2005) Tropical forests in a changing environment. Trends in Ecology & Evolution, 20, 553 – 560.

Chapter 2

Study Site and Datasets

Study Site

Mudumalai National Park

A majority of field work for this thesis was conducted in the Mudumalai National Park (hereafter Mudumalai, pronounced as MʊðʊməlɑI), a 321 sqkm of seasonally dry tropical forest situated in the Eastern, leeward side of the Western Ghats mountain range, India (a World Biodiversity hotspot). Dry tropical forests represent nearly half of the world's tropical forests, but are highly understudied compared to the moist tropical forests (Murphy & Lugo, 1986). Mudumalai presents a unique setting wherein along its ~40 km East–West stretch mean annual rainfall (MAR) varies by about 1000 mm rainfall (800 mm to 1800 mm MAR; Figure 1).

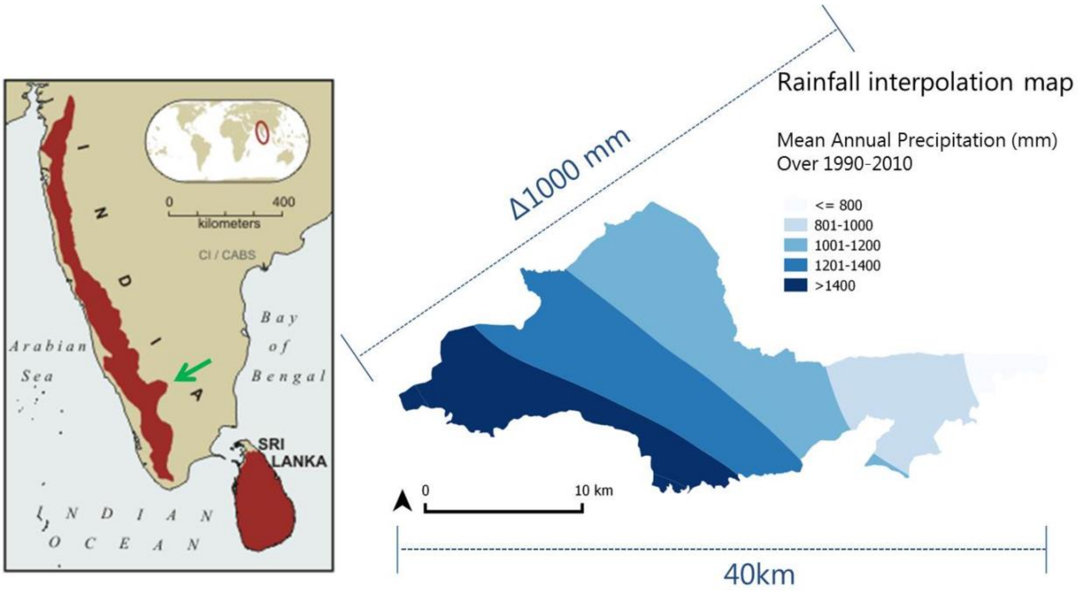


Figure 1: Mudumalai rainfall interpolation map. Inset (from the internet) shows in dark shade the Biodiversity Hotspot of the Western Ghats of India and Sri Lanka. Location of Mudumalai in the Western Ghats is indicated by an arrow.

Absence of a simultaneous temperature gradient and presence of a relatively flat terrain makes this rainfall gradient even more remarkable and useful for building plant response curves. Mudumalai receives showers from the South-East monsoon from June-September, and then again from November-December as the monsoon clouds hit and return from the Himalayas mountain range. The latter is termed as the returning or North-East monsoon. Seasonality in rainfall also varies along the gradient, with the Western side receiving 70 % of annual rainfall from the South-East monsoon and 30% from the North-East monsoon, while the Eastern side receives about half from each (Figure 2). Dry months (<100 mm rainfall/ month) are from November to April across the sanctuary (Figure 2).

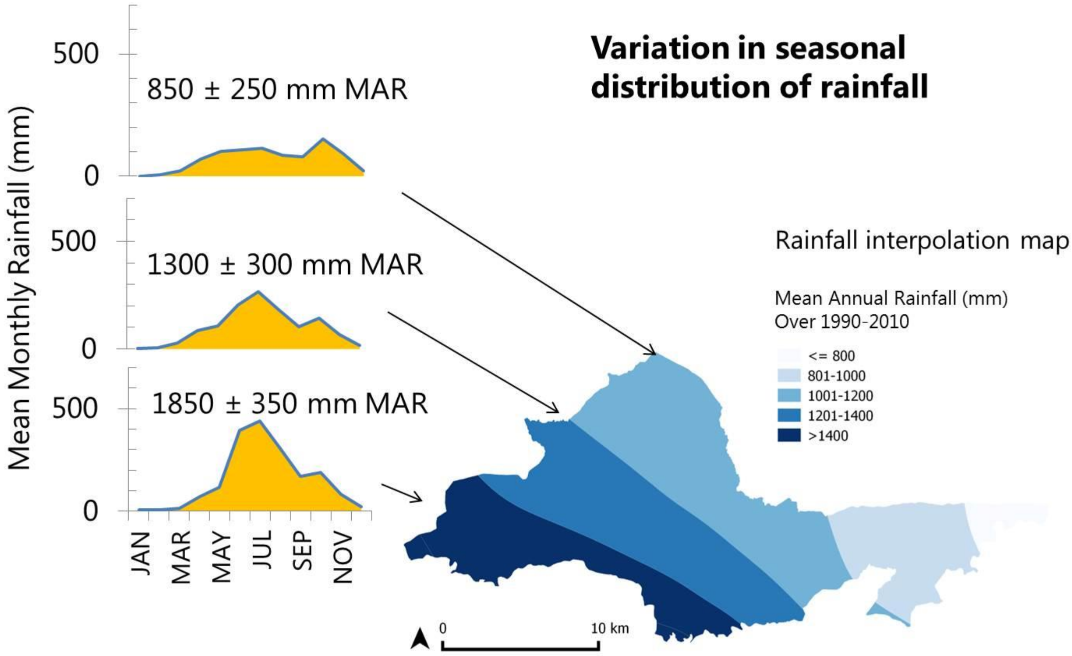


Figure 2: Variation in rainfall seasonality for three rain-gauge locations from the eastern, central and western side of Mudumalai.

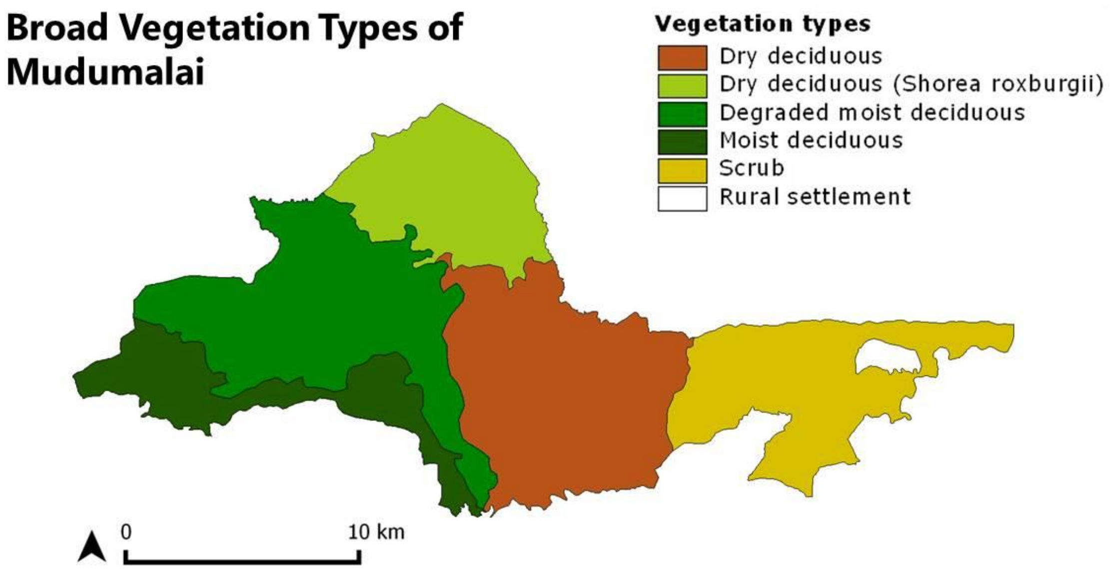


Figure 3: Broad vegetation types of Mudumalai. Map from Suresh et al. 2011.

Mudumalai shows a dramatic shift in forest types along its rainfall gradient (Figure 3): from tropical dry thorn (or dry scrub) on the eastern side (Figure 4a), through tropical dry deciduous at the center (Figure 4b) and tropical moist deciduous (or classified as degraded moist deciduous) in the western side (Figure 4c), with patches of tropical semi-evergreen forest found in the far West. Mudumalai experiences frequent, low intensity ground fires, with highest fire return frequencies in the tropical dry deciduous forest, given the

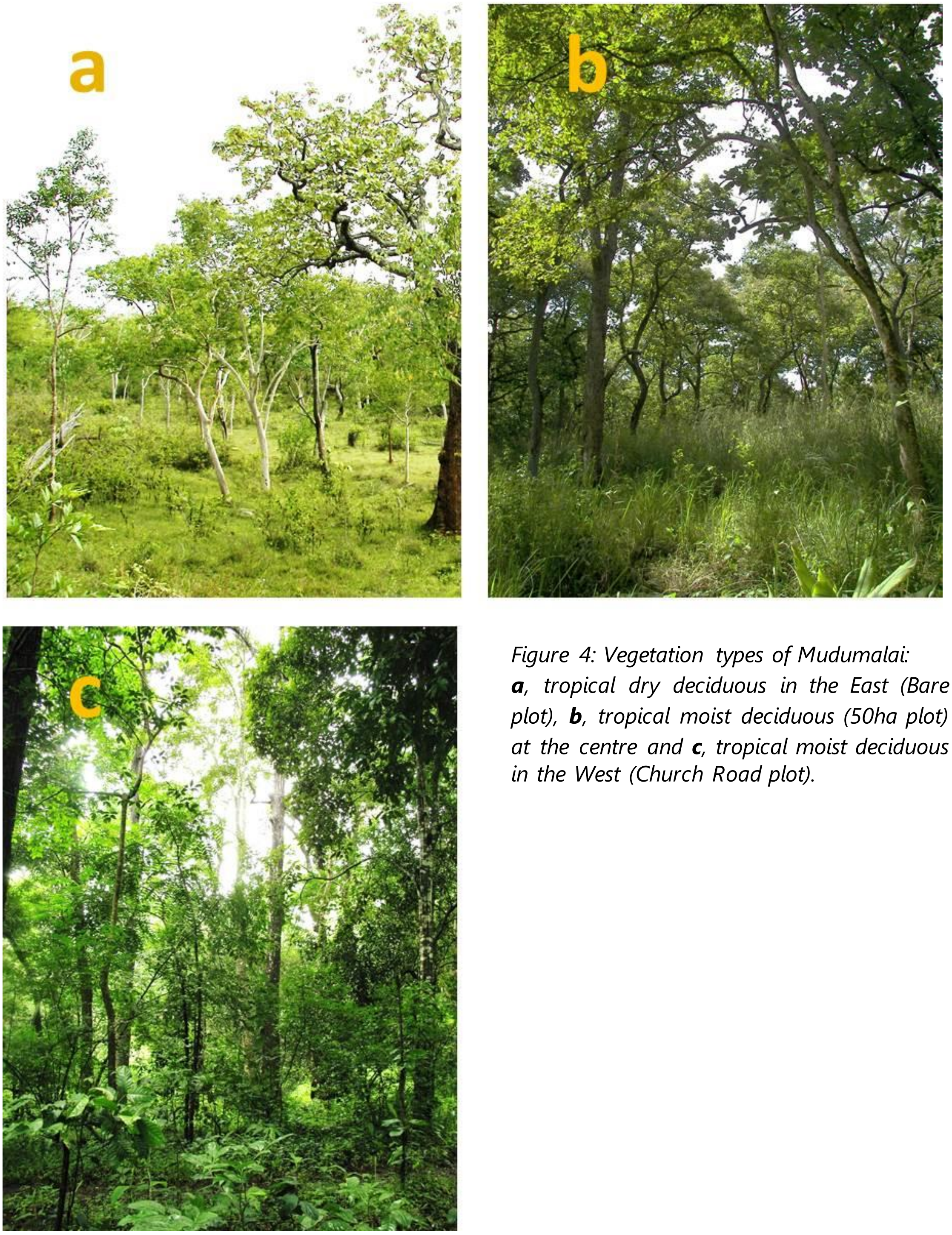


*Figure 4: Vegetation types of Mudumalai: **a**, tropical dry deciduous in the East (Bare plot), **b**, tropical moist deciduous (50ha plot) at the centre and **c**, tropical moist deciduous in the West (Church Road plot).*

high grassy biomass and dry-hot conditions in the summer (Mondal and Sukumar 2013; Figure 4b). Mudumalai serves as a sanctuary to one of the highest densities of large mammals in Asia including the Asian elephants (*Elephas maximus*), gaur (*Bos gaurus*), Axis deer (*Axis axis*), sambar deer (*Cervus unicolor*), tigers (*Panthera tigris*) and leopards (*Panthera pardus*; Sukumar et al. 2004, 2005).

In this setting, the Centre for Ecological Sciences, Indian Institute of Science has a network of long-term forest monitoring plots in Mudumalai since three decades: one 50-ha forest plot in the tropical dry deciduous forest and nineteen 1-ha plots spread across the sanctuary from East to West (Figure 5). The 50 ha forest plot is part of the CTFS-ForestGEO global network of tropical forest monitoring plots (Anderson-Teixeira et al., 2015; Condit, 1998; Sukumar et al. 1992, 1998, 2004). The 50ha plot and the network of 19 1-ha plots in Mudumalai have been established and monitored according to the CTFS-ForestGEO protocols (Condit, 1998).

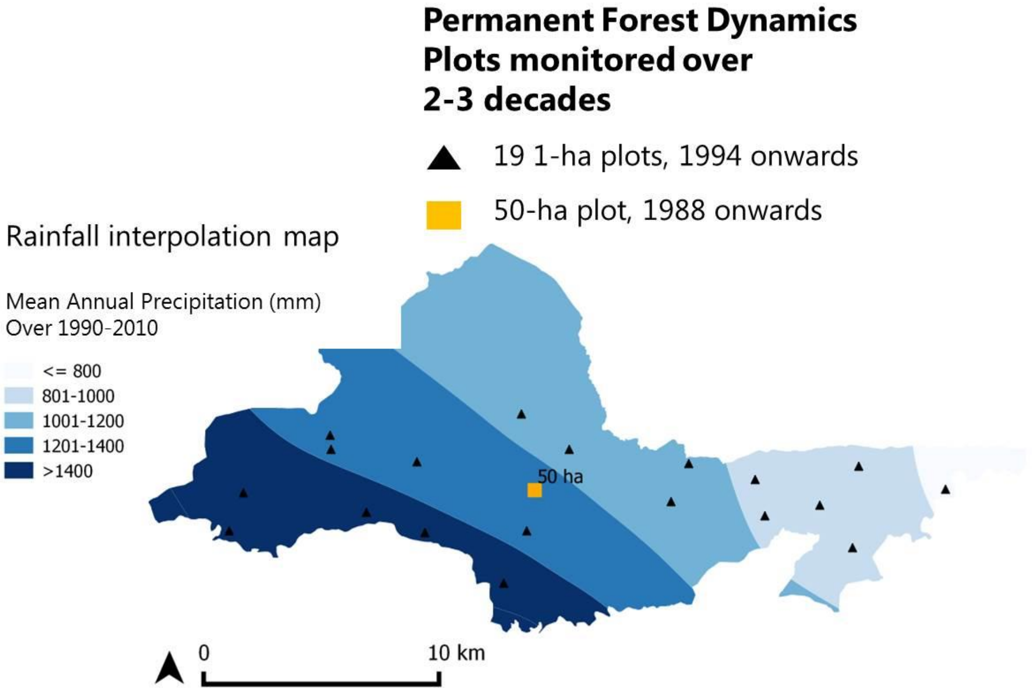


Figure 5: Locations of the permanent forest dynamics plots in Mudumalai National Park monitored by CES, IISc: one 50-ha plot (square), nineteen 1-ha plots (triangles).

Mulehole watershed

About 25 km from the Mudumalai 50 ha plot, in the Bandipur National Park, Karnataka the Indo-French Cell for Water Sciences, IISc (IFCWS) has been monitoring the Mulehole (pronounced as Mʊlehɘʊle) catchment environmental observatory *(11°44’N, 76°27’E)*. It is part of the ORE-BVET project (Observatoire de Recherche en Environnement – Bassin Versant Expérimentaux Tropicaux, http://bvet.omp.obs-mip.fr/index.php/eng/), supported by the French Institute of Research for Development (IRD), CNRS-INSU and Toulouse University. Situated in the dry deciduous forest, annual rainfall at Mulehole is approximately similar to that at the 50 ha plot in Mudumalai. The Mulehole catchment has been extensively monitored for hydrology (Ruiz et al. 2010, Parate et al. 2011), pedology (Braun et al. 2009), biogeochemistry (Riotte et al. 2014) and biophysics (Barbiero et al. 2007), among others.

Ainurmarigudi Forest plots

From late 70s through early 80s, Researchers at the French Institute of Pondicherry monitored tree growth in two 1-ha plots ~ 8 km north-west of Mulehole Watershed in the same rainfall regime at Ainurmarigudi (pronounced as a*eɪnu:rma:rɪgʊdi:*). In my limited knowledge this must be the first site in India where dendrometer bands were used to monitor tree growth.

Datasets used in this thesis

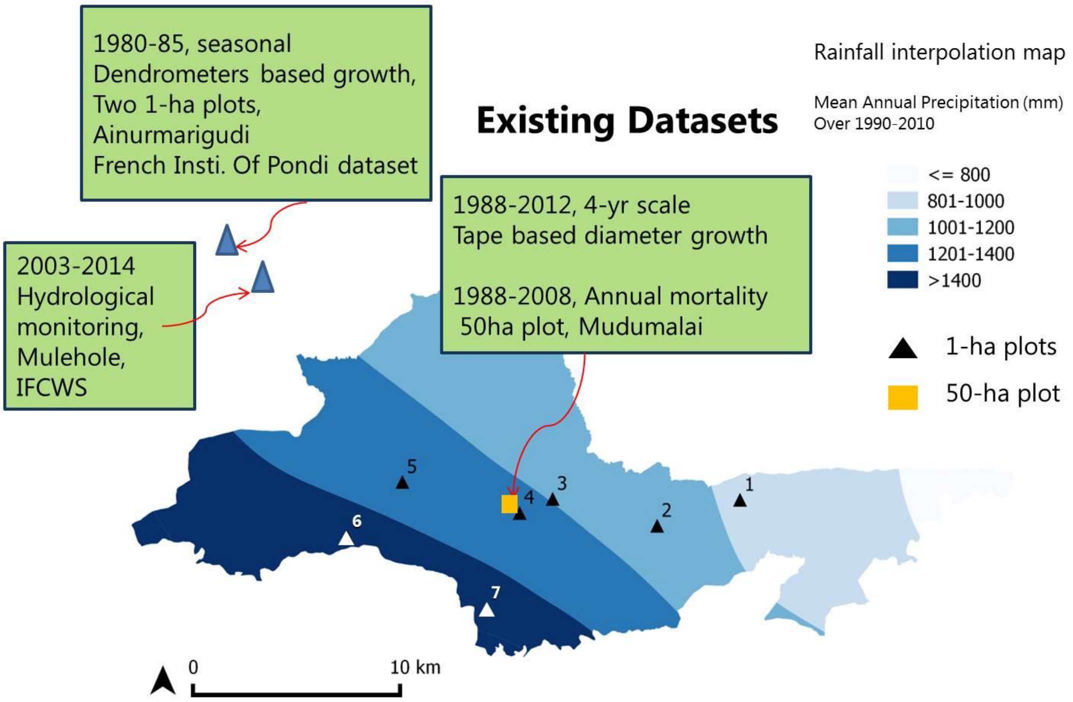
Existing Datasets

This thesis made use of some of the existing datasets on growth and hydrology available from Mudumalai, Mulehole and Ainurmarigudi (Figure 6): For Chapter 3 part I, seasonal tree growth dataset from Ainurmarigudi (1980-1985) collected by French Institute of Pondicherry was used. Chapter 3 part II, Chapter 4 and Chapter 5 used 4-year scale tree growth data from the 50 ha plot, Mudumalai (1992-2012) collected by CES, IISc. Chapter 5 used species mortality dataset from the 50 ha plot from 1988-2008 collected by CES, IISc. Chapter 5 also used the hydrology datasets from Mulehole collected by IFCWS, IISc to run a hydrological model at Mulehole and Mudumalai.

Collected Datasets

The datasets I collected during my PhD work have been used in Chapter 3 part II (tree-ring datasets from the 50 ha plot, Mudumalai), Chapter 4 (dendrometer datasets from seven 1-ha plots from the Mudumalai 1-ha plots network) and Chapter 5 (tree-ring datasets from Mulehole; Figure 7). The dendrometer dataset consists of seasonal and annual dendrometer time series from 2009-2013 on 800 trees across several species in the seven 1-ha plots.

Detailed descriptions of these datasets and study sites have been presented in the relevant chapters.


Existing Datasets

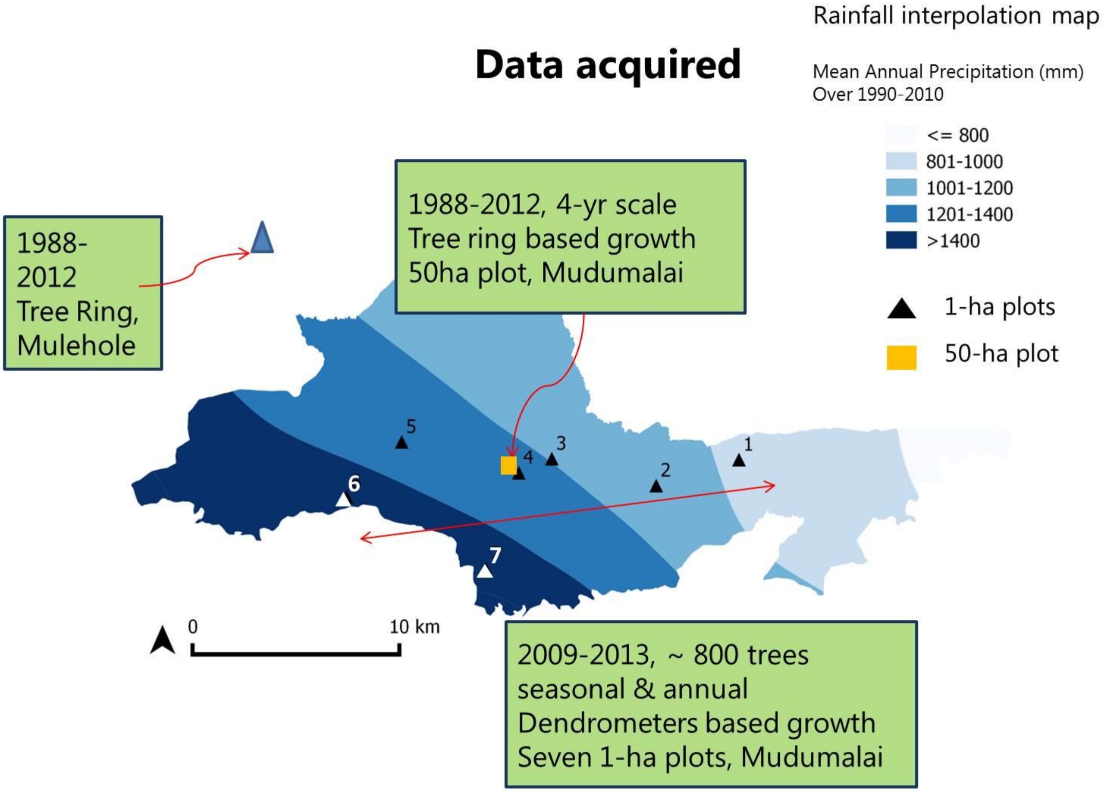
1980-85, seasonal
Dendrometers based growth,
Two 1-ha plots,
Ainurmarigudi
French Insti. Of Pondi dataset

2003-2014
Hydrological
monitoring,
Mulehole,
IFCWS

1988-2012, 4-yr scale
Tape based diameter growth

1988-2008, Annual mortality
50ha plot, Mudumalai

Figure 6: Location based descriptions of the existing datasets used in this thesis.



Data acquired

1988-2012 Tree Ring, Mulehole

1988-2012, 4-yr scale
Tree ring based growth
50ha plot, Mudumalai

2009-2013, ~ 800 trees
seasonal & annual
Dendrometers based growth
Seven 1-ha plots, Mudumalai

Figure 7: Location based descriptions of the collected datasets used in this thesis.

References

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer, J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S., Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M., Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J., Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K., Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena, D.M., Makana, J.-R., Malhi, Y., Marthews, T., Mat Serudin, R., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., de Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips, R.P., Sack, L., Sainge, M.N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J., Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., Zimmerman, J., 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Glob. Change Biol. 21, 528–549. doi:10.1111/gcb.12712

Barbiero, L., Parate, H.R., Descloitres, M., Bost, A., Furian, S., Kumar, M.S.M., Kumar, C., Braun, J.-J., 2007. Using a structural approach to identify relationships between soil and erosion in a semi-humid forested area, South India. CATENA 70, 313 – 329. doi:DOI: 10.1016/j.catena.2006.10.013

Braun, J.-J., Descloitres, M., Riotte, J., Fleury, S., Barbiéro, L., Boeglin, J.-L., Violette, A., Lacarce, E., Ruiz, L., Sekhar, M., Mohan Kumar, M.S., Subramanian, S., Dupré, B., 2009. Regolith mass balance inferred from combined mineralogical, geochemical and geophysical studies: Mule Hole gneissic watershed, South India. Geochim. Cosmochim. Acta 73, 935–961. doi:10.1016/j.gca.2008.11.013

Condit, R., 1998. Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer-Verlag, Berlin.

Mondal, N., Sukumar, R., 2013. Characterising weather patterns associated with fire in a seasonally dry tropical forest in southern India. Int. J. Wildland Fire.

Murphy, P.G., Lugo, A.E., 1986. Ecology of Tropical Dry Forest. Annu. Rev. Ecol. Syst. 17, 67–88.

Parate, H.R., Kumar, M.S.M., Descloitres, M., Barbiero, L., Ruiz, L., Braun, J.-J., Sekhar, M., Kumar, C., 2011. Comparison of electrical resistivity by geophysical method and neutron probe logging for soil moisture monitoring in a forested watershed. Curr. Sci. 100, 1405–1412.

Riotte, J., Maréchal, J.C., Audry, S., Kumar, C., Bedimo, J.P., Ruiz, L., Sekhar, M., Cisel, M., Chitra Tarak, R., Varma, M.R.R., Lagane, C., Reddy, P., Braun, J.J., 2014. Vegetation impact on stream chemical fluxes: Mule Hole watershed (South India). Geochim. Cosmochim. Acta 145, 116–138. doi:10.1016/j.gca.2014.09.015

Ruiz, L., Varma, M.R.R., Kumar, M.S.M., Sekhar, M., Maréchal, J.-C., Descloitres, M., Riotte, J., Kumar, S., Kumar, C., Braun, J.-J., 2010. Water balance modelling in a tropical watershed under deciduous forest (Mule Hole, India): Regolith matric storage buffers the groundwater recharge process. J. Hydrol. 380, 460–472. doi:10.1016/j.jhydrol.2009.11.020

Sukumar, R., Dattaraja, H.S., Suresh, H.S., Radhakrishnan, J., Vasudeva, R., Nirmala, S., Joshi, N.V., 1992. Long term monitering of vegetation in a tropical deciduous forest in Mudumalai, southern India. Curr. Sci. 62, 608–616.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Joshi, N.V., 1998. Dynamics of a tropical deciduous forest: population changes (1988 through 1993) in a 50-ha plot at Mudumalai, southern India.

Sukumar, R., Suresh, H.S., Dattaraj, H.S., John, R., Joshi, N.V., 2004. Mudumalai forest dynamics plot, India, in: Tropical Forest Diversity and Dynamics: Findings from a Large-Scale Plot Network. University of Chicago Press, Chicago, pp. 551–563.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Srinidhi, S., Nath, C., 2005. The dynamics of a tropical dry forest in India: climate, fire, elephants and the evolution of life-history strategies, in: Biotic Interactions in the Tropics, Ecological Reviews. Cambridge University Press.

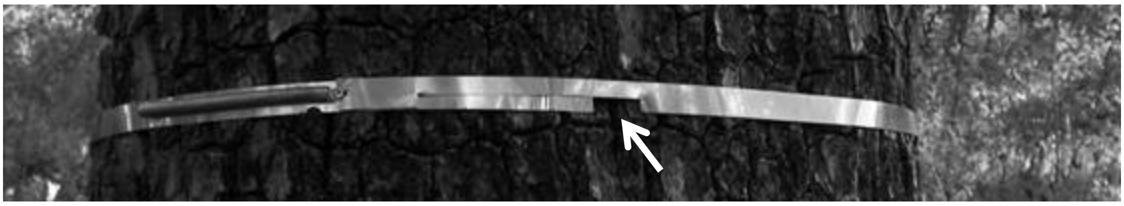
Chapter 3

The problem of hydrostatic stem-flexing in estimating tree growth and the timing of forest growth censuses

Introduction

As trees continue to deposit new wood in their trunks, their diameters are expected to increase. Diameter change measured at a fixed height on a tree stem at successive census intervals remains a simple and standard method to estimate tree growth in permanent sampling plots of forests (Condit, 1998; Sheil, 1995). Although woody growth is expected to be non-negative, negative growth is commonly reported in forest growth studies (Sheil, 1995). In the absence of any corrective measure and perhaps due to under-appreciation of the magnitude of error, it is usually ignored. As stem diameter changes not only due to woody growth, but also due to change in the water content in the stem (Fritts, 1961; Kozlowski and Winget, 1964) negative and even anomalous positive growth estimates are possible. Changes in water content in the stem occur mostly in the bark and external parenchyma of the stem, and not so much in the woody part of the trunk (Zweifel et al., 2000). Reversible stem-shrinkage may occur due to changes in stem water content at diurnal scales as the tree transpires through the day, while larger changes may occur at seasonal scales as the tree sub-surface water supply gets depleted (Kozlowski and Winget, 1964). Differences in water-status of the tree in successive measurement occasions can thus result into positive or negative bias in woody growth estimates for individual census intervals. The magnitude of the hydrostatic bias and its consequences on growth-resource or growth-climate relationship, however, remains under-appreciated.

Figure 1: A home-made stainless steel dendrometer band held around a Terminalia tomentosa tree stem with a stainless steel spring. White arrow depicts a window cut over an overlapping end of the band. As the stem expands or shrinks, the spring extends or shrinks and that is translated into increasee or decrease in the length of the window, which is in turn tracked manually using a vernier caliper.



In regions where the strongest variability in rainfall occurs at inter-annual scale—for example, under monsoonal climates—in order to evaluate influences of rainfall on tree growth, it is imperative to obtain a time series of tree growth at annual scale. Although tree ring based method is ideal for such a purpose, as it measures actual woody growth at annual scale, very few species in the tropics show anatomically distinguishable rings, nor is the method practical to employ at the whole stand level (Table 1). Methods that are employable across species estimate woody growth by tracking tree diameter change (Table 1). Among these methods dendrometer bands (Figure 1)—given their high precision—are used to estimate growth not only at annual, but sub-annual, as well as diurnal scales. However, given their monetary and maintenance costs these are employed at sub-stand level. Among the methods that are employed at the whole stand level, callipers with their greater precision are used to track trees of small size class (<5cm DBH), with growth rates typically in sub-millimetre range. Graduated tapes are used for larger sizes, but they have low precision (typically 1 mm resolution). Given the millimetre to sub-centimetre range of growth rates of tropical trees, graduated tapes can only be employed at supra-annual scale.

Table 1: Common methods to estimate tree growth with their actual object of measurement, advantages and drawbacks.

Method	**Measurement**	**Advantages**	**Drawbacks**
Tree Ring	Ring width using dendro-chronology	Retrospectively useful over centuries, Actual woody growth measured	Very few species in the tropics, Invasive, Annual scale
Graduated Tape or Caliper	Diameter change = Woody growth + water-induced stem flexing	Stand, All species	Supra-annual scale due to low resolution, Negative diameter change possible
Dendro-meter	Diameter change = Woody growth + water-induced stem flexing	Stand/sub-stand, All species, Annual/sub-annual/ diurnal scale	Negative diameter change possible

One may expect that the extent of hydrostatic bias may be insignificant at supra-annual scale. It would be also fair to expect that the extent of hydrostatic bias may increase from supra-annual to annual or sub-annual scale as the magnitude of hydrostatic change increases relative to woody growth. However, studies evaluating the extent of these biases at various scales and how they may affect inference on estimates of growth time series obtained from tree diameter censuses are crucially absent.

If dendrometers track diurnal stem diameter change, does unmatched timings in successive censuses introduce a hydrostatic bias in annual diameter change? Dendrometers are reported to underestimate diurnal stem shrinkage due to frictional delays (Sheil, 2003), but whether they underestimate seasonal shrinkage is not studied.

If dendrometers accurately track seasonal stem diameter change, does unmatched stem water-status due to differences in seasons or due to inter-annual variability in rainfall in successive censuses introduce a hydrostatic bias in annual diameter change? If annual dendrometer censuses are conducted at the end-of-wet season rather than dry season, does that avoid bias in growth estimates?

Here, we evaluate the extent of seasonal tree stem shrinkage and expansion in a Seasonally Dry Tropical Forest (SDTF) from a 5-year long dendrometer-based tree diameter census records, and ask whether the extent of hydrostatic bias can be a significant problem in estimating a time series of annual tree growth, especially when it is to be evaluated against variation in a resource or climatic conditions. We also asked at community level if hydrostatic bias can be avoided at supra-annual scale or by limiting diameter measurements to end-of-wet or dry season.

Additionally, we evaluate the extent of diurnal and seasonal reversible stem-shrinkages between one wet season and the following dry season with a method called Dawkin's Multiple Measures, which is an unbiased estimator of diameter change. Using simultaneous diameter change measurements by the dendrometer method, I evaluate if dendrometers can accurately track diurnal and seasonal diameter changes. These observations are then used to assess how they may influence bias in growth estimates in dendrometer censuses, and their timing schedule.

Materials & Methods

Extent and variability in seasonal reversible shrinkage in 5-yr long census records

To analyze extent of seasonal water-induced fluctuations in dendrometer-based diameter time series, I made use of the longest continuous dendrometer band seasonal record in this region that was collected by French Institute of Pondicherry, India (IFP) from 1980 through 1985 (unpublished data, IFP) in Ainurmarigudi. This period also included the strongest known El-Niño drought that occurred in the year of 1983. Ainurmarigudi is located ~8 km from the Mulehole Check Post, Bandipur National Park, Karnataka, and is a Tropical Dry Deciduous forest with *Tectona grandis* L. f., *Anogeissus latifolia* (Roxb. ex DC.) Wall. ex Guillem. & Perr., *Grewia tilifolia* Vahl, *Dalbergia latifolia* Roxb. *Terminalia crenulata* Roth., as the dominant tree species. In March 1980, at a 0.4 ha plot in Ainurmarigudi, home-made stainless steel band dendrometers were installed at 130 cm DBH on 126 trees belonging to 14 species that were larger than 10 cm DBH. While the initial diameter was measured using a graduated tape with 1 mm resolution, dendrometer measurements were taken using a vernier caliper (0.2 mm precision) every month until April 1982, and then every third month until February 1985. A time-series of cumulative community-wide diameter increment was plotted (Figure 2).

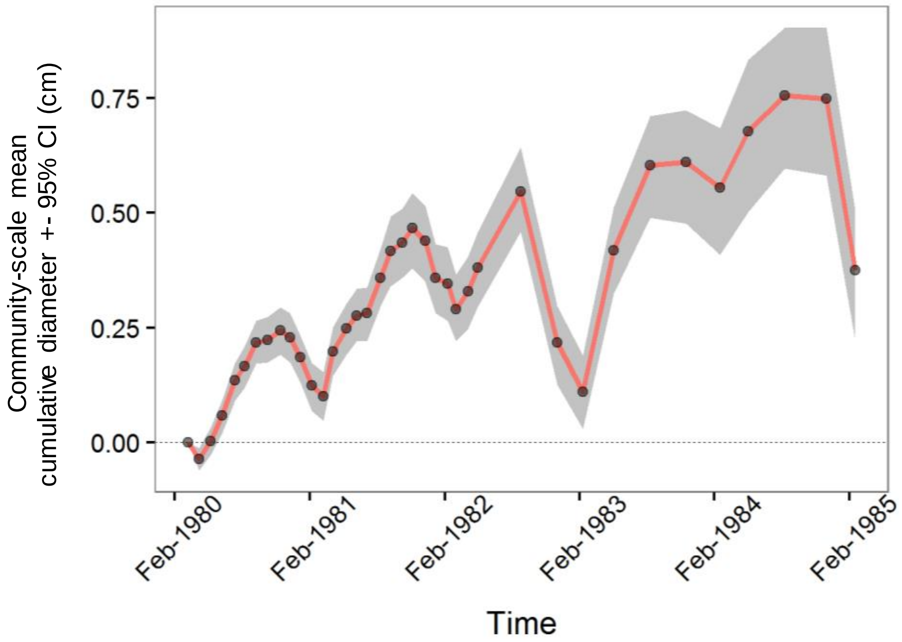


Figure 2: Community-wide mean cumulative diameter at Ainurmarigudi from February 1980 through February 1985 is shown by the red curve. Dark circles depict when censuses were conducted: monthly censuses until April 1982, followed by censuses every three months. Grey envelope depicts 95% bootstrapped confidence interval.

Extent of diurnal and seasonal shrinkage and accuracy of dendrometers

To analyze whether dendrometers accurately capture diurnal as well as seasonal reversible stem shrinkage, at both these scales, I compared the dendrometer method with that of Dawkins' Multiple Measures (DMM) to estimate diameter change (Dawkins, 1956; Sheil, 2003). For this I took measurements using both the methods on 75 trees belonging to 5 common species from three 1-ha plots along the rainfall gradient on which dendrometer bands were already installed in the summer of 2009. These included two tropical dry deciduous forest plots—Circular Road (plot 2; 1100 mm MAP from 1990-2010) and one from the 50 ha plot (plot 3; 1100 mm MAP)—and one tropical moist deciduous forest plot—Munde Mule (plot 5, 1325 mm MAP); see Chapter 2, Figure 6. For the DMM, eight marked paths were drawn on each tree—four above and four below the dendrometer band at 10 cm from each other (Figure 3). These paths were measured by a graduated tape (1 mm resolution) while an observer made sure that the tape followed the marked path. Mean across the eight measured circumferences, converted to diameter was considered as the diameter estimated by the DMM method.

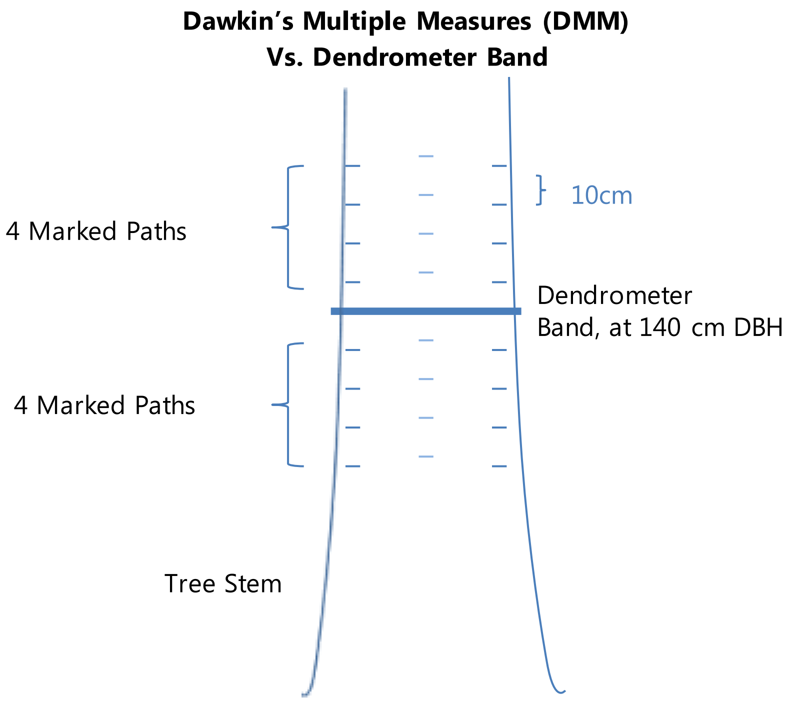


Figure 3: Conceptual drawing for stem diameter measurement by two methods: dendrometer and DMM.

Dendrometer measurements were taken by digital caliper (Mitutoyo Digimatic (Japan), Accuracy: 0.02 mm). For each tree, stem measurements were taken by both the methods—DMM and dendrometer—immediately one after another. These censuses were taken in the morning of November 2010, and then in the morning (8:00 to 11:30) and afternoon (12:35 to 14:15) of April 2011, with all the trees measured in the same order across censuses. Seasonal and diurnal changes in diameter obtained by both the methods were then compared at the population level (Figure 4). To estimate diurnal changes at the end-of-wet season, which I could not do in November 2010, censuses were carried out during morning (9:30 to 11:15) and afternoon (13:13 to 13:53) of November 2012 on a subset of 32 trees from the above trees. Observations on the moist deciduous forest plot could not be taken in this census. We used censuses done on the above 75 trees by both DMM and dendrometer methods in January 2011 and February 2012 (between 10:00 to 13:00) to get an estimate of annual growth.

In all the above calculations, successive diameters using dendrometer measurements were calculated by iteratively optimizing the following equation (http://richardcondit.org/data/dendrometer/calculation/Dendrometer.php):

$$D_{t+1} = D_t - \arcsin(C_t/D_t) \times D_t/\pi + \arcsin(C_{t+1}/D_{t+1}) \times D_{t+1}/\pi$$

Where, C_t, C_{t+1} are the successive chords on the tree circumference measured by the dendrometers and D_t, D_{t+1} the diameters at time t and $t+1$.

All analyses were done in R statistical environment, version 3.0.2 (R Core Team, 2013).

Results & Discussion

Extent and variability in seasonal reversible shrinkage in 5-yr long census records

In the community-wide cumulative diameter increment curve at Ainurmarigudi (Figure 2), large, periodic, reversible stem shrinkages were observed during the dry season of every year from 1980-1985. The timing and extent of these reversible shrinkages were highly variable from year to year. Diameter was seasonally most expanded in November for both the years 1980-81 and 1981-82 for which records were available monthly, while most shrunk diameters were either for April (1980) or March (1981, 1982), but for year 1984-85 diameter peaked in August not November. Reversible shrinkage was especially prominent in the El-Niño drought year of 1983 in which nearly all the diameter increment accumulated in the two previous years was lost in one dry season. This rules out the possibility that hydrostatic bias may be insignificant at supra-annual scales, and emphasizes that the amount of bias depends on the water-status of trees between the two censuses being compared.

Diameter change calculated from dry season of 1982 to dry season of 1983 would thus be highly negative, while that from dry season of 1983 to dry season of 1984 would be highly positive, but erroneously so, with woody growth being underestimated and overestimated in these years, respectively. Annual diameter change calculated from successive end-of-wet-season measurements, e.g. November/December, by which time woody growth may be complete in this seasonally deciduous forest, would also lead to a similar problem. Thus hydrostatic bias in growth estimates cannot be avoided by choosing a particular season.

Extent of diurnal and seasonal shrinkage and accuracy of dendrometers

As measured by the DMM method, diurnal changes (i.e. from morning to noon) in stem diameter were one fifth in magnitude as compared to seasonal changes from November, which is nearly at the end of wet season, to April in the dry season (Figure 4, Table 1). Dendrometers reported very little shrinkage on the diurnal scale compared to the DMM method (Figure 4a). However, at the seasonal scale, dendrometers showed similar extent of shrinkage as that measured by the DMM method (Figure 4b).

For the subset of 32 trees that were measured in the end-of-wet season in November 2012, while DMM showed triple the diurnal change as that showed in dry season, dendrometers showed similar changes as that in dry season (Table 1). The seasonal changes shown by either the 75 trees or the subset of trees were in the same order of magnitude as that of annual changes for both the DMM as well as dendrometer method.

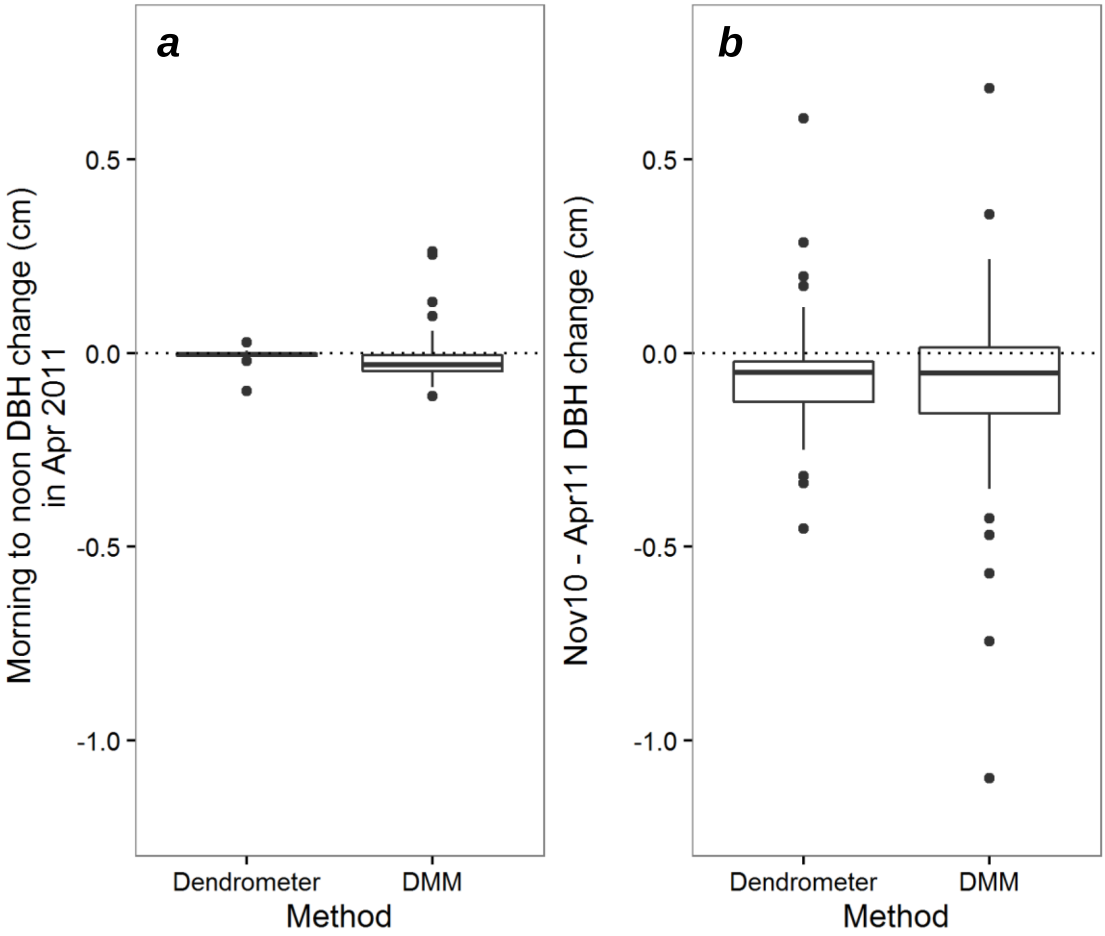


Figure 4: Boxplots of diurnal (a) and seasonal (b) change in diameter as measured by Dendrometer and DMM method on 75 trees. Each data point represents observation from a single tree. The bottom and the top of the boxes represent the lower and the upper quartile, the bands in the middle represent the median. Lower and upperends of the whiskers extend to 1.5 times the interquantile range (the length of the box) from the box. Dark circles are observations beyond this range. Note the difference in vertical axis scale for the two plots.

Table 1. Diameter changes observed by DMM and dendrometer at various temporal scales. Mean and 95% CI of the mean changes are reported in cm. 95% CI are basic intervals obtained from ordinary bootstrapping using the package boot in R.

a) For the set of 75 trees from three plots:

Scale of change	**From**	**To**	**DMM**		**Dendrometer**	
			Mean	**95% CI**	**Mean**	**95% CI**
Diurnal, Dry season	Apr 2011, morning	Apr 2011, afternoon	-0.018	[-0.031, -0.005]	-0.005	[-0.007, -0.002]
Seasonal	Nov 2010	Apr 2011	-0.087	[-0.133, -0.039]	-0.102	[-0.161, -0.015]
Annual	January 2011	February 2012	0.256	[0.188, 0.316]	0.16	[0.034, 0.304]

b) For the subset of 32 trees from two dry deciduous forest plots:

Scale of change	**From**	**To**	**DMM**		**Dendrometer**	
			Mean	**95% CI**	**Mean**	**95% CI**
Diurnal, End-of-wet season	Nov 2012, morning	Nov 2012, morning	-0.043	[-0.059, -0.024]	-0.005	[-0.010, -0.001]
Diurnal, Dry season	Apr 2011, morning	Apr 2011, afternoon	-0.015	[-0.041, 0.005]	-0.007	[-0.009, -0.005]
Seasonal	Nov 2010	Apr 2011	-0.103	[-0.137, -0.064]	-0.095	[-0.124, -0.064]
Annual	January 2011	February 2012	0.248	[0.124, 0.346]	0.264	[0.143, 0.360]

The greater variance in DMM method compared to dendrometer at diurnal and seasonal scales may be attributed to lower precision arising from manually running the graduated tape around the tree girth multiple times, unlike in the case of dendrometer, which is a spring-loaded steel band fixed around the girth of the tree, and given the lower resolution of the graduated tape for DMM of 1 mm compared to 0.01 mm for the digital caliper used for the dendrometers.

This suggests that while dendrometers may underestimate reversible stem shrinkage at the diurnal scale, at the seasonal scale they may be capturing reversible stem shrinkage much accurately. The extent of diurnal shrinkage as captured by dendrometers is two orders of magnitude smaller than the seasonal change captured by them. This suggests that differences in the time of the day at which successive censuses are conducted is unlikely to introduce a significant hydrostatic bias in estimating growth at seasonal or annual scale. However, the extent of reversible stem shrinkage tracked by dendrometers at seasonal scale is in the same order of magnitude as that of annual diameter change. Therefore, we suggest that diameter changes measured at annual scale quite faithfully report the water-status of the tree in the seasons they are measured. As the water-status of trees are mostly unmatched across annual censuses—the case study of Ainurmarigudi being a most striking example—we conclude that annual growth estimates from stem diameter change are thus hydrostatically biased, and these biases can be large. The exact extent of the hydrostatic bias in the estimate of time series of woody growth needs to be carefully evaluated and corrected, especially if the latter is to be evaluated against time series of resources or climatic conditions.

Acknowledgements

We are thankful to the French Institute of Pondicherry (IFP), India for making available the Ainurmarigudi dendrometer census dataset. Special thanks are due to Raphael Pellissier for generously providing these, and to Matthieu Cisel for visiting IFP, Pondicherry and obtaining these datasets from old reports. We thank Tamil Nadu Forest Department for permissions to work in Mudumalai National Park. Ministry of Environment and Forest, India financially supported fieldwork in Mudumalai, and Council for Science and Industrial Research, India supported RCT with Junior and Senior Research Fellowships.

References

Condit, R., 1998. Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer-Verlag, Berlin.

Dawkins, H.C., 1956. Rapid detection of aberrant girth increment of rain-forest trees. Emp. For. Rev. 35, 448–454.

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Australia.

Sheil, D., 2003. Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by dendrometer bands. Can. J. For. Res. 33, 2027–2035. doi:10.1139/x03-121

Sheil, D., 1995. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. For. Ecol. Manag. 77, 11–34. doi:10.1016/0378-1127(95)03583-V

Chapter 4

And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations

---

This chapter is published in its present form as:

Chitra-Tarak, R., Ruiz, L., Pulla, S., Dattaraja, H.S., Suresh, H.S., Sukumar, R., 2015. And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations. *Forest Ecology and Management*. 336, 129–136.

Abstract

Accuracy in tree woody growth estimates is important to global carbon budget estimation and climate-change science. Tree growth in permanent sampling plots (PSPs) is commonly estimated by measuring stem diameter changes, but this method is susceptible to bias resulting from water-induced reversible stem shrinkage. In the absence of bias correction, temporal variability in growth is likely to be overestimated and incorrectly attributed to fluctuations in resource availability, especially in forests with high seasonal and inter-annual variability in water. We propose and test a novel approach for estimating and correcting this bias at the community level.

In a 50-ha PSP from a seasonally dry tropical forest in southern India, where tape measurements have been taken every four years from 1988 to 2012, for nine trees we estimated bias due to reversible stem shrinkage as the difference between woody growth measured using tree rings and that estimated from tape. We tested if the bias estimated from these trees could be used as a proxy to correct bias in tape-based growth estimates at the PSP scale.

We observed significant shrinkage-related bias in the growth estimates of the nine trees in some censuses. This bias was strongly linearly related to tape-based growth estimates at the level of the PSP, and could be used as a proxy. After bias was corrected, the temporal variance of growth rates of the PSP decreased, while retaining the effect of exceptionally dry or wet periods, indicating that at least a part of the temporal variability arose from reversible shrinkage-related bias. We also suggest that the efficacy of the bias correction could be improved by measuring the proxy on trees that belong to different size classes and census timing, but not necessarily to different species.

Our approach allows for reanalysis – and possible reinterpretation – of temporal trends in tree growth, above ground biomass change, or carbon fluxes in forests, and their relationships with resource availability in the context of climate change.

Introduction

Accuracy in tree woody growth estimates is critical to global carbon budget estimation and climate-change science (Clark and Kellner, 2012; Malhi, 2012). The most commonly and widely used method for estimating tree growth in permanent sampling plots (PSPs) involves the measurement of successive stem diameter changes using a graduated tape or a dendrometer band, and is followed by the use of allometric equations (Chave et al., 2014, 2005) to estimate the above-ground biomass (AGB) and carbon of the plot and changes therein (Condit, 1998; Marthews et al., 2012). However, biases and uncertainties in the measurements in PSPs can potentially substantially affect estimates of forest tree growth, and thus AGB and carbon pools and fluxes (Cushman et al., 2014; Muller-Landau et al., 2014; Sheil, 1995; Talbot et al., 2014).

Water-induced expansion and shrinkage of tree trunks poses a major challenge in the accurate measurement of woody diameter change (Sheil, 2003, 1997). This is because diameter change as measured by a tape or a dendrometer band not only arises from irreversible woody growth (cell wall extension and cell division), but also from reversible expansion and shrinkage in the stem due to water-induced fluctuations. Bias in woody growth estimates due to this reversible stem flexing occurs if the water status of the tree is different across successive measurements (Baker et al., 2002; Sheil, 1995). In the absence of bias correction, temporal variability in growth rates is likely to be overestimated and wrongly attributed to fluctuations in resource (e.g. water) availability. To our knowledge, such biases have not been satisfactorily estimated so far, as no study has measured and separated actual woody growth from water-induced fluctuations at the level of forest community, and no satisfactory method of correcting this bias at this scale is currently available.

Diameter change due to reversible stem flexing occurs as the stem tissues storing water reversibly constrict due to dehydration. This is induced by reduced xylem water potential, which is determined by transpiration demand and below-ground water availability. Depending on the species, the largest fraction of the reversible stem flexing is known to occur in the bark (Zweifel and Häsler, 2001) or in the outer parenchyma – the tissues in between the cambium and the cork (Scholz et al., 2008). A water potential difference between xylem and bark causes a radial flow of water from the stem storage compartment towards the xylem, causing the stem bark diameter and consequently the stem diameter, to shrink. The xylem contributes much less to the reversible flexing, although it likely stores and supplies water for about 10–50 % of daily transpiration demand (Holbrook and Zwieniecki, 2011).

Much variation in reversible stem flexing occurs with respect to species and in time due to variations in environmental factors affecting water stress, as reviewed by Baker et al. (2002). Temporal variation occurs at a diurnal scale as tree stems typically contract during the day when leaves transpire, and rehydrate during the night (Karling, 1934; Klepper et al., 1971). At a seasonal scale, stem shrinkage during the dry season occurs due to high transpiration demands and depletion of the soil water reserve. Species differ in the extent and timing of reversible stem flexing (Kozlowski and Winget, 1964; Scholz et al., 2008). This is possibly due to differences in timing of leaf flush, flowering or fruiting (Baker et al., 2002), and differences in tissue structures, and/or in relative proportions of various tissues - causing differences in water storage capacity and/or volume change per unit change in water content (Scholz et al., 2008). In the absence of leaves, water stored in the trunk may last across seasons, enabling rehydration of stem tissues and subsequent flowering or flushing (Borchert, 1994a, 1994b; Holbrook and Zwieniecki, 2011). The extent and timing of shrinkage within a species can differ according to topographic position and rooting depth, which influences access to water (Borchert, 1994b; Markesteijn et al., 2010; Meinzer et al., 1999). The effect of tree size on the direction and extent of reversible flexing is debated (Baker et al., 2002). In summary, diameter change in stems can arise not only from woody growth, but also from water-induced reversible flexing, which we henceforth refer to as “water growth”.

The case that biases in growth estimates of PSPs could arise from short term – diurnal and seasonal – water-induced fluctuations was first made by Sheil (1997). Negative tree growth estimates are commonly reported in dry forests, which are attributed to water growth and are considered biases (Sheil, 1995). Reversible stem flexing has long since known to be substantial compared to irreversible woody growth and thermal changes (Kozlowski, 1971). The extent of seasonal shrinkage varies from year to year (Baker et al., 2002; Pélissier and Pascal, 2000), and is likely to lead to substantial biases in growth estimates based on annual or supra-annual censuses (Baker et al., 2002; Pélissier and Pascal, 2000). We expect that the largest biases in growth are likely in forests where both high seasonal and inter-annual variability is observed, as often found in seasonally dry tropical forests (SDTFs) (Maas and Burgos, 2011).

A few studies have tried to use a measure of short-term water availability such as rainfall or soil moisture and transpiration demand to account for water growth. Sheil (1997) observed that growth rates of most stems in an Ugandan semi-deciduous forest showed an apparent reduction when measured over wetter seasonal periods, presumably due to measurements during the wetter season being typically made on drier, bright, sunny days when trees are in full leaf and diurnal shrinkage is high. Soil water potential at the time of measurement explained the bias in annual growth estimates in a two year study in a semi-deciduous forest in Ghana (Baker et al., 2002).

Prescriptions for the optimal timing of annual diameter measurements to minimize bias due to diurnal & seasonal water growth have been controversial for seasonally dry forests. For example, Pélissier & Pascal (2000) suggested that inter-annual variation in dry season shrinkage might be stronger than wet season expansion, and therefore recommended measuring growth in the wet season in order to minimize bias in annual growth measurements. Baker and others (2002) observed greater inter-annual variability in diameter change during the dry season, and also prescribed the wet season for measuring annual growth. However, Sheil (2003) claimed that observations by Baker and others (2002) of higher variability in diameter change in dry season was debatable, given measurement errors of dendrometer bands and exceptional drought conditions in that study. Sheil (2003) suggested that "wet season measures are more perturbed by moisture (deficits and availability) and by phenological events (flowers, fruit etc.) impacting true growth. Dry season quiescence reduces growth variance".

However, these hypotheses have remained untested in the absence of actual measurements of the two components of diameter change - woody growth and water growth. Tree ring widths can provide a measure of actual woody growth at annual scale. However this method is invasive, and also expensive in terms of required expertise and resources. Thus estimating bias at community level needs other approaches.

In this study we propose a novel approach for estimating and correcting bias in growth estimates due to water-induced fluctuations at the community level. We used long-term diameter census data from a PSP in a southern Indian seasonally dry tropical forest. Comparing woody growth using tree rings and observed growth using a tape in a small number of trees, we check whether significant biases in tree growth estimates were due to water growth. We then test whether biases in this small number of trees can be used as a proxy to correct biases in tree growth at the community level. We also suggest ways to improve this approach.

Materials & Methods

Study site, climate and forest plot

We used data from a 50-ha Mudumalai Forest Dynamics Plot (MFDP) located in a seasonally dry tropical forest in the Western Ghats, southern India (Latitude: 11.5989, Longitude: 76.5338). Detailed information on this forest and the 50-ha plot can be found elsewhere (Sukumar et al., 1998, 1992; Suresh et al., 2013, 2010). The average annual precipitation 4km from the site is 1200 (± 280 SD) mm from 1988 to 2013 (Figure 1).

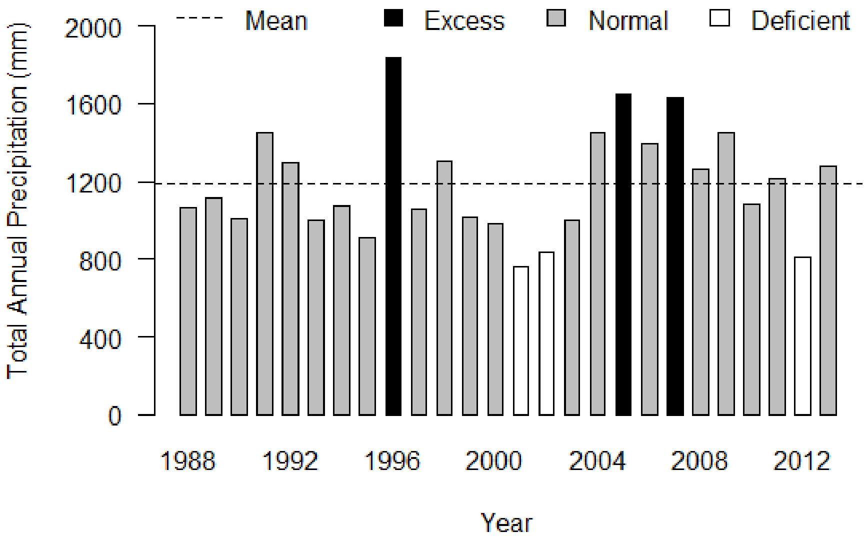


Figure 1: Total annual precipitation at Kargudi, 3km away from the 50 ha MFDP. Data for the year 1988 and 1989 has been derived from a regression between Kargudi and Gamehut rainguage records (Nath et al., 2006). Mean Annual Precipitation (MAP) during the study period, from 1988 to 2013, is shown with a dotted line. Years with excess (>120% MAP) and deficient (<70% MAP) precipitation are highlighted. The study period ended in March 2013. Precipitation during January to March 2013 was 23.6 mm.

About 80% of annual precipitation occurs during the monsoon from June to November. The dry period (<100mm precipitation/month) lasts for about 6-8 months, with four months of less than 50 mm precipitation/month from December to March. Average monthly maximum and minimum temperatures are 27.4°C (± 2.7 SD) and 16.4°C (± 2.0 SD) respectively. The forest type is classified as tropical dry deciduous by Champion & Seth (1968) and Puri (1960). Most trees are deciduous from January to March (Murali and Sukumar, 1993; Prasad and Hegde, 1986; Suresh and Sukumar, 2009).

Tape-based growth censuses for the 50-ha MFDP

In the 50-ha plot all woody plant stems >10 mm have been censused for diameter at breast height (1.3 m, DBH) every four years, from 1988 to 2012 (Table 1). These stems are mapped, tagged with a unique number, identified to species (or morpho-species), measured for DBH with a graduated tape/caliper (1-mm resolution) following the Centre for Tropical Forest Science protocols (Condit et al., 1999). Each census typically began in June and took about 6 to 9 months to complete (Table 1), maintaining the same sequence of enumeration - from 1st to 50th hectare from the south-west to north-east end of the 0.5 km x 1 km plot. However, the first census in 1988 continued for one full year, whereas census in 1996, which followed a fire earlier that dry season, was completed within 3 months. DBH measurements were typically carried out between 9 am and 2 pm, in effect restricting diurnal variation in DBH, for we observed maximum shrinkage during late afternoons (unpublished results).

Table 1: The beginning, end date, and duration of each growth census at the 50ha MFDP, and exact dates of census for the cored nine trees. Years for which rings of the nine trees are included to calculate ring growth for each census- interval are given.

Census	Enumeration Start date	Enumeration End date	Census Duration (Months)	Census dates for the selected 9 trees	Rings included in the interval
1988	19 May 1988	12 May 1989	12	02, 04, 12 May 1989	
1992	09 Jun 1992	02 Dec 1992	6	19, 20 Nov, 21 Dec 1992	1989-1992
1996	25 Jun 1996	21 Sep 1996	3	14, 15, 21 Sep 1996	1993-1996
2000	01 Aug 2000	19 Dec 2000	5	14, 15, 19 Dec 2000	1997-2000
2004	08 Aug 2004	02 Dec 2004	5	30 Nov, 02 Dec 2004	2001-2004
2008	09 Jun 2008	07 Mar 2009	9	19, 20, 21 Feb, 07 Mar 2009	2005-2008
2012	15 Jun 2012	09 Mar 2013	9	25, 27 Feb, 07 Mar 2013	2009-2012

In this study, we only used trees that were present in all censuses in order to avoid bias due to the turnover of individuals and species and due to large changes in the size-class distribution. Further, we chose only trees with single stems in order to avoid bias due to swapping of diameter measurements of multiple stems (individual stems were not tagged). This subsample will be referred to as the "community-level" set hereafter. Diameter change (in cm) during each census interval was annualized by dividing with inter-census period, i.e. four years. We identified "spike" growth values in each tree's record that lay outside the mean ± 3*standard deviation range based on the remaining growth values in its census history, and whose absolute value was greater than 1 $cm.yr^{-1}$. We also considered growth rates with magnitudes greater than 4 $cm.yr^{-1}$ as unrealistic or erroneous. In both cases we removed the corresponding trees from the dataset in order to retain a fixed set of trees across all censuses. The "community-level" set contained 9016 trees. These represent nearly half of the trees ever present in the 50-ha plot. The rest half was left out mostly because they were dynamically present.

Measuring woody growth using tree rings in a sample of trees

For measuring woody growth, we selected nine seemingly healthy and straight-boled trees from the MFDP in the 30-60 cm DBH size class belonging to three species - *Tectona grandis* L. f. (*n* = five), *Terminalia crenulata* Roth. (*n* = three), and *Lagerstroemia microcarpa* Wt. (*n* = one) that show distinguishable annual rings and rank among the top four dominant canopy species in the plot (Sukumar et al., 2004). There were hardly any common species that showed distinguishable rings. We couldn't collect more sample sizes for *Lagestroemia microcarpa* or *Terminalia crenulata* for trees of *L. microcarpa* were too hard to core, or cores did not show sufficiently distinguishable annual rings. The latter was observed even for *T. crenulata*. The sampled nine trees were located within 80 m of each other in the north-east end of the MFDP and thus have been consistently measured in the last phase of each census, typically, during or after December (Table 1). As a consequence, barring the 1996 census when measurements were done in September, in all other censuses they were measured mostly in their deciduous stages. This ensured that annual growth in the census year was complete. For the 1996 census, a fraction of woody growth is likely to have occurred after the census measurement in mid-late September, but only until leaf fall in December as, for example, it is known that in *Tectona grandis* the cambium is dormant during the leafless period (Rao and Dave, 1981). However not more than 1/5th of annual growth is likely to have occurred during this period given that the leafy period is from April to December, and the period with mature leaves extends from July to December.

For each tree, cores of about 100 mm long and 5 mm in diameter were taken in three to five radial directions at the height of 125 cm from the tree base in October 2013. The openings left on the trees due to the coring were then sealed with wax. After polishing the cores, rings were dated and their widths measured with an increment measuring machine coupled with a stereo-zoom microscope (0.01 mm accuracy). For each tree, yearly ring widths from three to five collected cores were pooled together and twice the average of these widths was taken to represent woody growth in diameter for the given year. For each tree, the mean annual woody growth during each census interval was calculated by taking the average of woody growth in diameter for all the growth years during the census interval, as detailed in Table 1.

Data analyses: measuring bias in tape-based growth estimates in the cored trees

For this analysis we assumed that the difference between tape-measured and ring-measured diameter change was due to water-induced fluctuations, although some part of the difference could also originate from other sources such as bark addition/removal/injury, and measurement errors. We write:

Tape-measured diameter change = Water-induced diameter change + Ring-measured diameter change

For simplicity, we refer to the above terms as:

Tape growth = Water growth + Ring growth

To examine whether or not water growth explains tape growth or ring growth, we performed linear regressions between these variables, tested the significance of the slope and intercept, and examined the proportion of explained variance. We also examined whether or not mean water growth was significantly different from zero across censuses and for each census separately, using the Student's *t*-test.

Data analyses: estimating and correcting bias in tape growth at the community-level using bias in the cored trees as a proxy

We first tested if census-interval-wise mean tape growth for the "community-level" tree set had a significant linear relationship with census-interval wise mean water growth for the nine trees ($n = 6$ census intervals), specifically by verifying whether or not the slope of the linear regression was significantly different from zero. Since the slope was significant (see Results section 3.2), we subtracted slope effect of the water growth from the corresponding tape growth value for each tree in the community level set to obtain an estimate of woody growth.

Data analyses: examining effect of measurement time, diameter and species of the cored trees in estimating bias in community-level tape growth

We prepared three subsets of the "community-level" tree set in order to examine the effect of the choice of cored trees – with respect to measurement time, tree diameter and species identity – on the effectiveness of bias correction. The "community-level" censuses had been carried out over six to nine months, and thus were likely to include large variations in tree water status over time, compared to the nine trees selected for coring. The first subset therefore only included trees that were censused within ± 1 month of the census dates of the nine trees (Table 1). This set of trees is likely to have undergone similar changes in water status as the nine cored trees, and is hereafter referred to as the "census-duration restricted" set (n = 1535 trees), The second subset only included trees from the "community-level" set that were in the same size class (> 20 cm DBH, n = 5841) as the cored set. This was called the "large" tree set (for reference, the remaining trees (i.e. 1-20cm DBH) were called the "small" tree set). The third subset only included trees from the "community level" set that belonged to the species as the cored set. This was called the "selected-species" set (n = 5715 trees). For each of these three subsets, we fitted linear regressions between the census-interval wise mean water growth of the cored trees and census-interval wise mean tape growth of the set. We expected the slopes of these linear regressions to be higher than the slope of the regression for the full "community-level" set. ,

All analyses were done in R statistical environment, version 3.0.2 (R Core Team, 2013).

Results

Bias in growth estimates in the cored trees

For the nine cored trees, all six census-intervals together, variability in water growth was about double that in ring growth, but similar to that in tape growth (Figure 2a). Water growth was not related to ring growth (Figure 2b, Table 2). Tape growth was found to be a poor predictor of ring growth (Figure 2c, Table 2). Water growth, however, showed a significant linear relationship with tape growth and also explained large proportion of the variance therein (Figure 2d, Table 2). This suggests that most of the variability in tape growth arose from water-induced fluctuations and measurement errors. All six census-intervals together mean water growth was not significantly different from zero. This indicates that all censuses together, mean tape growth was not a biased estimator of ring growth.

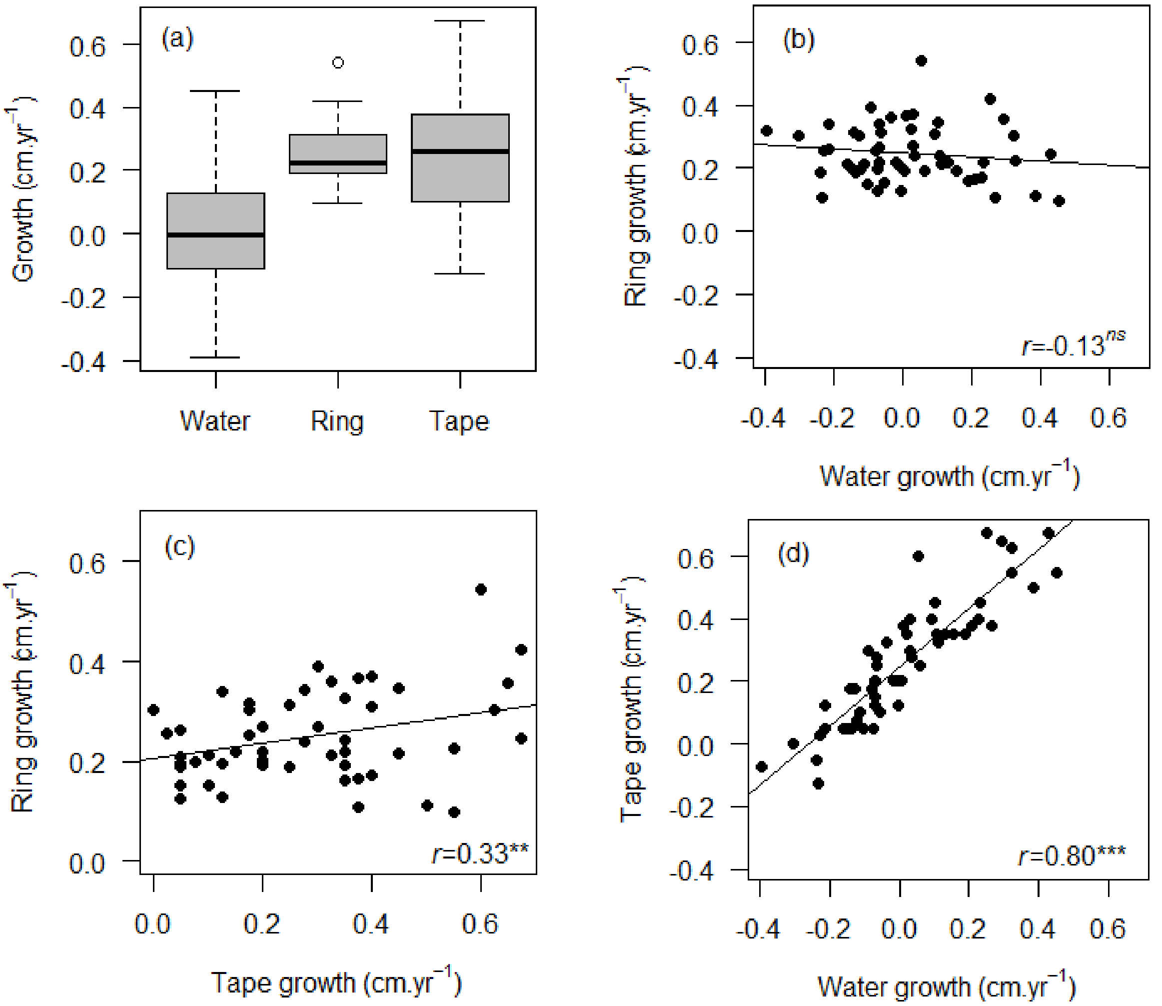


*Figure 2: Comparison between tape, ring and water growth in the nine cored trees, all six census intervals pooled together (9 x 6 = 54 data points). (a) Distribution of tape, ring and water growth. The median (black line), interquartile range (IQR) (upper and lower limits of the boxes; 75 and 25 percentile), and variation extending to 1.5 times the IQR (whiskers) are given. Associations between (b) ring & water, (c) ring & tape, and (d) tape & water growth. Regression line and Pearson correlation coefficients and their level of significance are given. ns, non-significant; *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001.*

Table 2: Relationships between tape, ring and water growth in the nine cored trees. Effect sizes, goodness-of-fit (adj. r squared values) and p-values are given.

Linear regression	Adj. R squared	p-value
Ring growth = -0.06 * Water Growth + 0.24	-0.002	0.36
Ring growth = 0.21* Tape Growth + 0.15	0.09	0.01 **
Tape growth = 0.94 * Water Growth + 0.25	0.80	<0.001 ***

Census-interval wise (Figure 3a), both tape and ring growth displayed significant variations in some years, but contrasting temporal patterns. However, mean water growth was significantly different from zero only for the first two census intervals, and not the last four (Figure 3b). The variance in water growth remained high in each of the censuses.

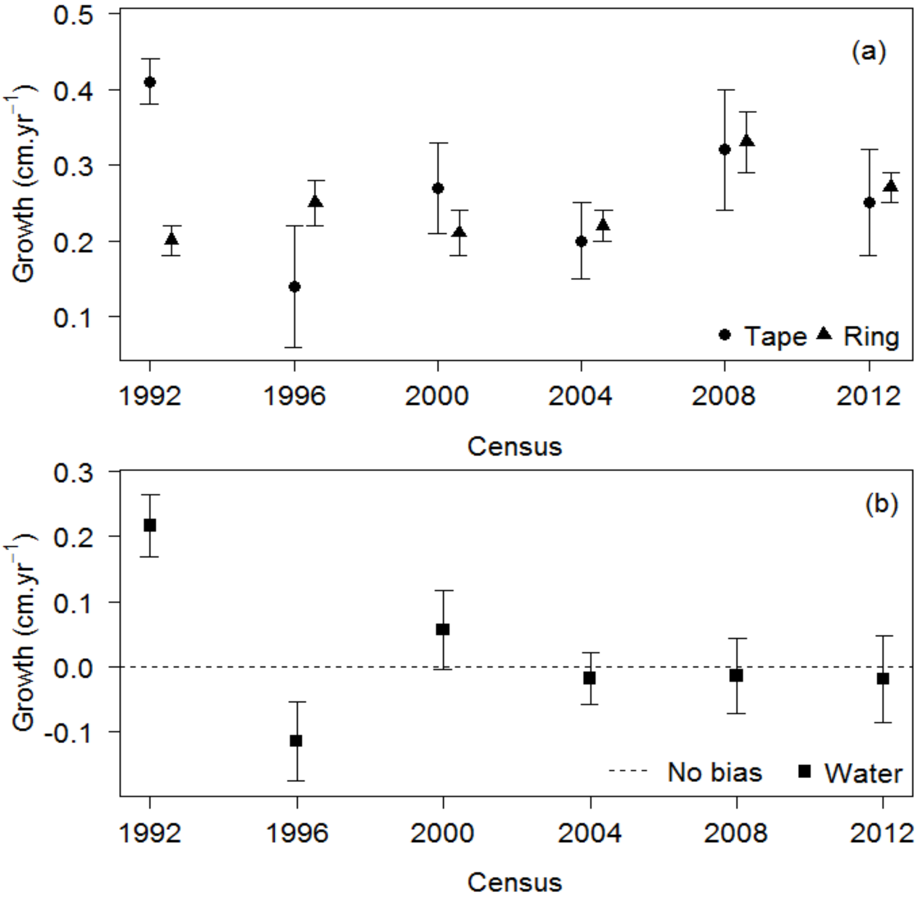


Figure 3: (a) Ring versus tape and (b) water growth for the nine cored trees for each four yearly census interval. Mean with standard error bars are given.

3.2 Estimating & correcting bias in tape growth at the community-level using bias in the cored trees as a proxy

Mean water growth of the nine trees in each census had a significant linear relationship with census-interval wise tape growth of the "community-level" tree set (Figure 4), suggesting that water growth even measured for a few trees can be used as a proxy for bias in growth estimates of trees at the "community-level" that are censused over six to nine months.

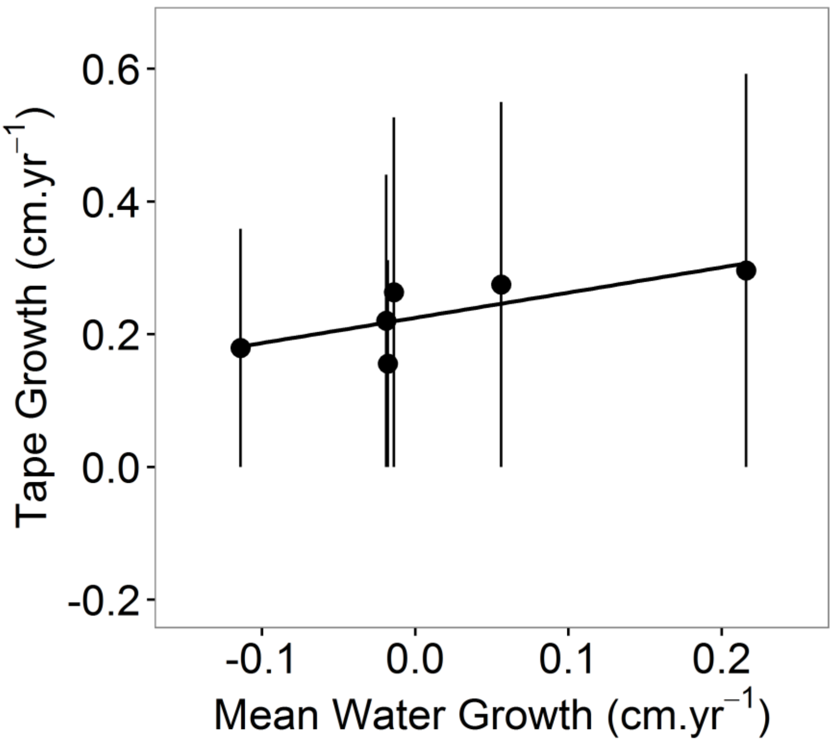


Figure 4: Regression between census-wise tape growth at the "community-level" for 50ha PSP in Mudumalai and water growth of the nine trees in the plot. Mean tape growth with standard deviation bars are given for each census-interval. Mean slope = 0.3800 and 95% bootstrapped CI = [0.3524, 0.4078], p-value <0.001.

Before bias correction, mean tape growth across census-intervals was 0.247 cm.yr^{-1} with a standard deviation of 0.47 cm.yr^{-1} (Figure 5a). Mean growth for census interval 1988-1992 and 1996-2000 was higher than the mean growth for 2004-2008, and mean growth for 2000-20004 was lowest, while that for 1992-1996 second lowest. After bias correction, mean growth across censuses was 0.237 cm.yr^{-1}, with a standard deviation of 0.23 cm.yr^{-1}. Thus the coefficient of variation in census-interval wise mean growth reduced by 50% (Figure 5b: from 0.190 to 0.097) and that for median by about 20% (from 0.167 to 0.137).

After bias correction, the 2004-2008 census-interval emerged as the one with the highest mean growth, while census-interval 2000-2004 remained as the one with the lowest mean growth, and emerged as the only interval with significantly lower growth than the mean growth across intervals (Figure 5b). Mean growth for census-interval 1988-1992 and 1992-1996 emerged close to the mean growth across census-intervals. Bias correction had a much stronger effect on mean/median tape growth for the first three censuses than for the last three. This was expected because mean water growth in the nine cored trees in the last three censuses was close to zero, but highly positive or negative in the earlier censuses (Figure 3b).

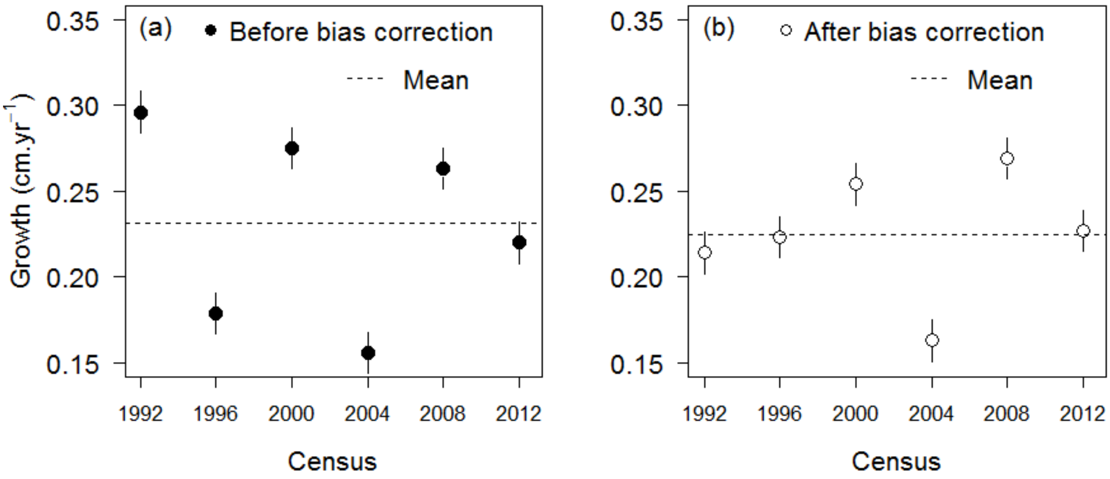


Figure 5: Tape growth at "community-level" for the 50 ha MFDP (a) before and (b) after bias correction for each census. Mean and error bars showing SE are presented. Dashed line represents mean growth rate across censuses.

Examining effect of measurement time, diameter and species of the cored trees in estimating bias in community-level tape growth

As in the case of "community level" tree set, for all the other subsets defined earlier, namely, "census-duration restricted", "selected-species", "large" and "small" tree sets, we found a significant linear relationship between census-interval wise tape growth for trees in each of these groups and the proxy for bias, that is, the census-interval wise mean water growth in the nine trees. The slope of this linear relationship for the "census-duration restricted" & "large" tree set was significantly higher than the slope for the "community-level" tree set, but not for the "selected-species" tree set. The slope for the "large" tree set was also significantly higher than that for the "small" tree set (Figure 6). This suggested that water growth measured based on the nine cored trees as a proxy was more efficient in reducing bias in growth estimates of trees censused close in time (and also in space) to the cored trees and also similar in size to the cored trees, but not more efficient for species that were used for coring.

Discussion

While all census-intervals together for the cored nine trees, a large proportion of the variance in tape growth was attributable to water growth (Figure 2d), census-interval wise analysis showed significant positive or negative bias only in the first two censuses, although variance among trees for a given census was large in all censuses (Figure 3b). The fact that the mean of census-interval wise water growth in the cored trees showed significant linear relation with census-interval wise tape growth at the "community-level" suggests that water growth measured in a few trees can be used as a proxy for estimating bias in tape growth at the scale of the tree community (Figure 4).

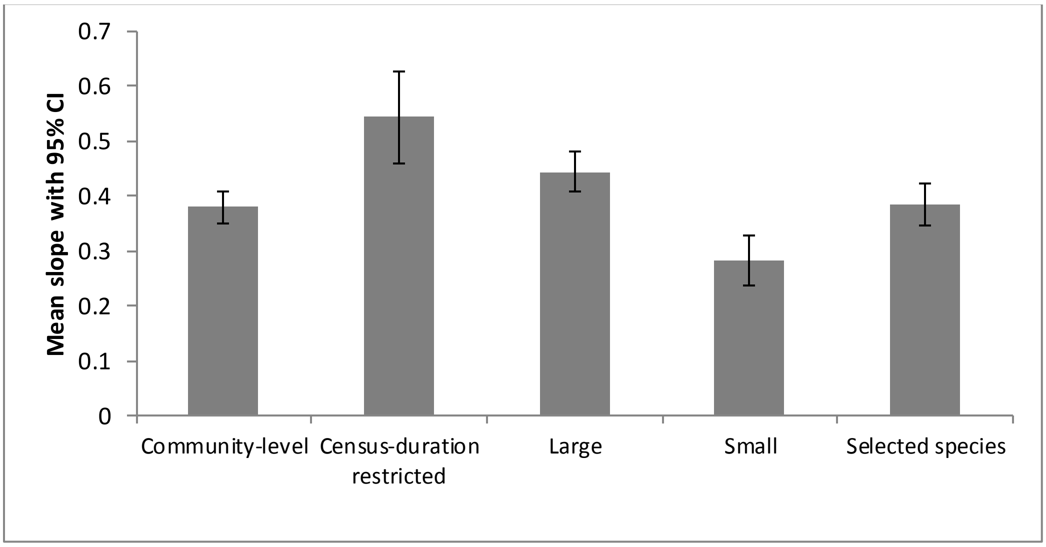


Figure 6: Comparison between slopes of the linear relationship between census-wise water growth in the nine cored trees and each of the tree sets – "community-level", "census-duration restricted", "large" and "small", and "selected species". Means and 95% bootstrapped confidence intervals of the slopes are given.

The novelty of the proposed proxy for tree water growth is that it is directly estimated from trees, unlike the proxies suggested so far – based on rainfall or soil moisture - which are indirect (Baker et al., 2002; Sheil, 1997). While environmental data such as rainfall, PET, or soil moisture may or may not be available throughout the census period, tree ring data could be obtained retrospectively even several years after the survey is over, and would be useful for reinterpreting datasets where bias could not be avoided.

At the "community-level", detrending reduced the bias in growth estimates due to water-induced fluctuations, which reflected in the reduction in coefficient of variation in mean and median tape growth rates across census intervals. After bias correction mean tape growth rate for 2004-2008 census-interval emerged as the highest relative to all other censuses, while 2000-2004 mean tape growth rate emerged as the lowest. As 2004-2008 interval was the most resourceful in terms of rainfall (Figure 1), and witnessed the highest water table levels in the last 50 years, as estimated by Ruiz et al. (2010) in a nearby forest, woody growth in this interval was expected to be the highest. On the other hand 2000-2004 census - interval included two of the strongest droughts in the last century, and thus woody growth during this interval was expected to be the lowest. These results are important indication that the proxy was able to reduce growth variations among periods, while highlighting exceptionally dry or wet periods.

Water flux related biases in growth estimates are also likely to pose problems in our understanding of general ecological theory. For example, in a pan-tropical assessment of allometric relationships between growth rates and tree diameter (Muller-Landau et al., 2006), most plots showed consistent relationships across years, except for the driest forest plot – that happens to be the 50-ha MFDP. Here, large trees showed contrasting allometric relationship between consecutive census intervals, namely, 1992-1996 & 1996-2000. Nath and others (2006) attributed the difference in growth rates in these censuses to difference in rainfall. We found that after correcting for bias this difference between large and small trees reduced substantially (Figure 7), suggesting that to a large extent this anomalous behavior may have arisen from over- or under-estimation of growth in the successive census intervals due to fluctuating water status of the trees.

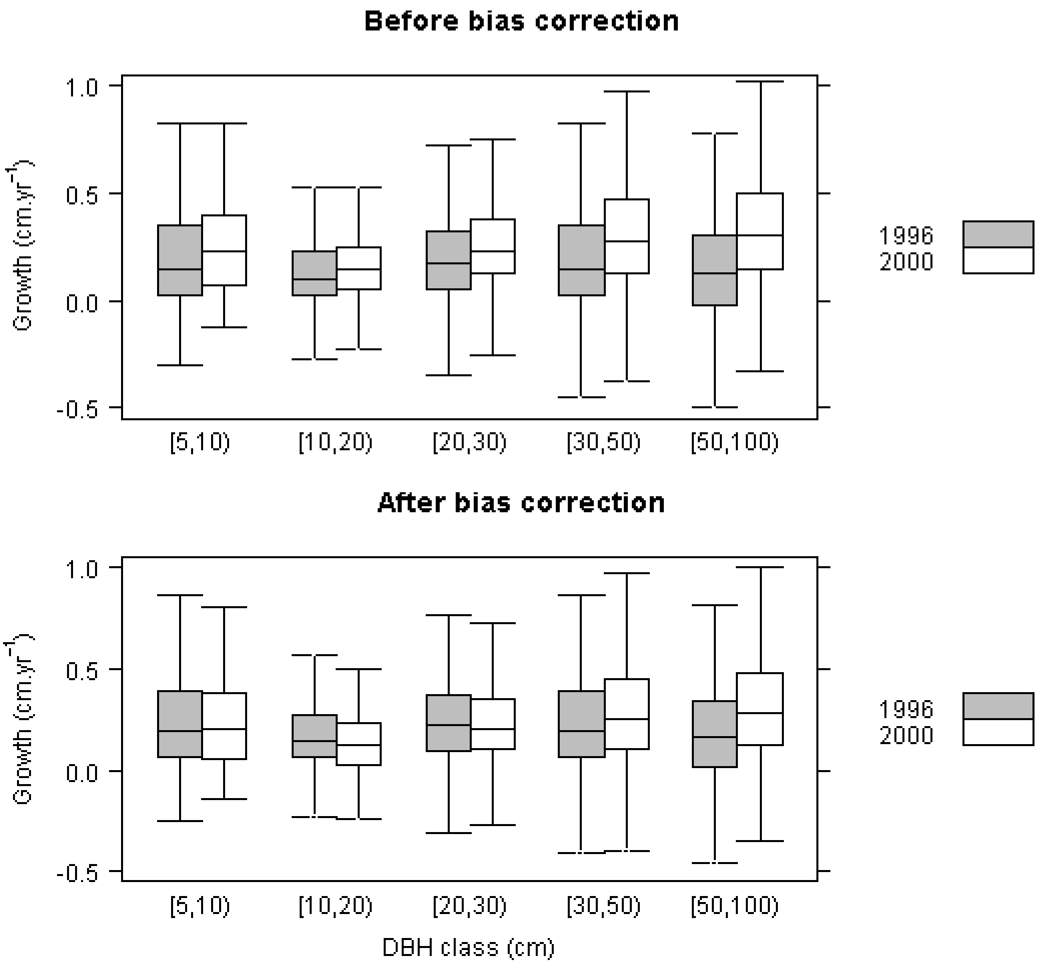


Figure 7: Comparison of growth rates for census 1996 and 2000 according to size class before and after bias correction. The median (black line), interquartile range (IQR) (upper and lower limits of the boxes; 75 and 25 percentile), and variation extending from 5 to 95 percentile (whiskers) are given. Outliers are not shown.

This study tried to identify several sources of errors that cause bias in tape growth estimates, namely, measurement season, measurement time of the day, diameter and species. Although measurement errors are also possible, they are more likely to bias growth estimation when methods are inconsistent over time (Sheil, 1995), which was not the case here. Thus the observed biases are likely to have come from water-induced fluctuations. Diurnal water-induced fluctuations in the stem could potentially have contributed to observed biases (Sheil, 2003). However, this is likely to be marginal, because in a separate study (unpublished results), we observed that seasonal variations in stem diameter are about three times higher than diurnal variations, and diurnal fluctuations were observed mostly in the late afternoon, while the present survey was carried out from 9 am to 2pm.

The efficacy of the proposed proxy is likely to increase by including trees representing the wide temporal range in census duration, or in the present case, various regions of the 50-ha MFDP, as indicated by the steeper slope of the relation between proxy and tape growth for the census-duration restricted set over the "community-level" trees set. The efficacy of the proxy is also likely to improve by including trees from various size classes and correcting their biases separately, as the proxy was most effective for trees that were of the same size class as that of the trees that were used for developing it. Including a larger variety of species may or may not improve the efficacy of the proxy, as the tape growth - proxy relationship did not improve when applied over only those species that were used for developing the proxy. The strength of the proposed proxy is not so much in it being representative of the whole community or explaining all the variance in water-induced fluctuations at the community level, as it is in its ability to capture the community-level potential water bias in each census. It might be surprising for community ecologists to define a proxy based on such a small set of trees as was done in this study, but proxies by definition are not meant to be completely representative; for example, a rainfall time series from a single rain-gauge does not represent all the spatial variation in water availability over a site but could still be effective in capturing the signal of temporal water availability.

Researchers have been seeking the best season of the year – wet or dry - in seasonal forests for annual or supra-annual diameter measurements to minimize water-induced biases, but have reached contrasting and debatable conclusions (Baker et al., 2002; Sheil, 2003). A separate study at the study site (unpublished results) indicated that biases- as measured from water growth remained and were not significantly different from each other irrespective of whether the wet or dry season was chosen for annual diameter measurement. This is perhaps because variation in water status in these trees remained high in either of the seasons, possibly mediated via variation in soil moisture, potential evapotranspiration. Also, the time in the year where variations in tree water status are minimal can vary from year to year, depending on weather conditions. Thus, whichever season tree growth is measured in, a correction would be necessary in order to estimate diameter growth without bias due to water-induced fluctuations. The proposed proxy, by trying to estimate the bias rather than avoiding it, is thus useful to end the conundrum of searching the season of least bias.

A large part of the variability remained unexplained by the proxy both at the "census-duration restricted" level as well as at the "community-level". This is understandable because change in water status is a function of a large number of factors - including species specific material properties of stem tissues, actual water availability as a function of precipitation in the recent past, soil properties, topography. Future work could include development of more effective proxies, possibly including several environmental variables and species-specific properties.

The results suggest that at least a part of the observed temporal variability in tape growth in this seasonally dry tropical forest arises from bias due to water-induced fluctuations. Especially in seasonally dry tropical forests, temporal growth variation gets almost exclusively attributed to temporal environmental variability and is explained as growth response to fluctuation in availability of resources, water in particular (Feeley et al., 2007; Nath et al., 2006; Toledo et al., 2011; Wagner et al., 2014). Correcting water growth induced biases in tree growth estimates would help in establishing actual woody growth–resource relationships. Corrections applied to biases in the community/PSP level tree growth estimates in time could also substantially improve our understanding of carbon budgets of these forests and the effects of climatic and global changes on the temporal variation in biomass and carbon stocks and fluxes.

Conclusions

The results suggests that water growth measured in a few trees in each census - measured as the difference between diameter changes using tape and ring – can be effective in estimating bias in growth estimates due to water-induced fluctuations and measurement error at the community level. After bias correction the variability in mean growth rates across census-intervals decreased, while the effect of exceptionally dry or wet periods was retained, indicating that at least a part of the observed temporal variability in growth rates arose from reversible, water-induced fluctuations. This approach allows for reanalysis – and possible reinterpretation – of temporal trends in tree growth, above ground biomass change, or carbon fluxes in forests, and their relationships with resource availability in the context of climate change.

Acknowledgements

We thank the Tamil Nadu Forest Department for permissions to carry out this research. RCT received a CSIR PhD student fellowship and RS was a J. C. Bose National Fellow during the course of this study. Special thanks are due to our staff in Mudumalai field station, especially Kunmari, M. Bomman, B. Bomman, M. Rajan, drivers and cooks for long-term field work and support. Suggestions from Sandeep Pulla improved the statistical analyses. RCT is especially thankful to many stimulating discussions and advice from Laurent Ruiz that strengthened this manuscript. Comments from two anonymous reviewers on an earlier draft improved this manuscript.

Corrigendum

In the main text errors in in the independent variable were not incorporated in building several linear relationships, some of which are used subsequently in other linear relationships, and thus the error should be propogated.

The revisions of some of the figures below demonstrate a correction of this error. Note that the key method described in the text is thus improved with the addition of confidence interval of the estimates, but the key conclusions remain the same.

Table 2 revised: Liner mixed effect model equivalents for relationships presented in Table 2 in the main text to account for autocorrelation due to repeated measures. Relationships between tape, ring and water growth in the nine cored trees in linear mixed effects model framework are thus given with tree as fixed effect. Effect sizes, goodness-of-fit (Conditional R-sq) and p-value approximations are given. CIs for slope and intercept are are obtained from 95 percentile intervals based on 1000 non-paramteric bootstrap replicates of corresponding linear regession.

Linear relationship between fixed effects	CI for Slope	CI for Intercept	Conditional R^2	p-value
Ring growth = -0.06 * Water Growth +	[0.225,	[-0.175, 0.074]	0.5	0.275
Ring growth = 0.095* Tape Growth +	[0.226,	[-0.184, 0.075]	0.5	0.069
Tape growth = 0.94 * Water Growth +	[0.224,	[0.818, 1.082]	0.9	<0.001

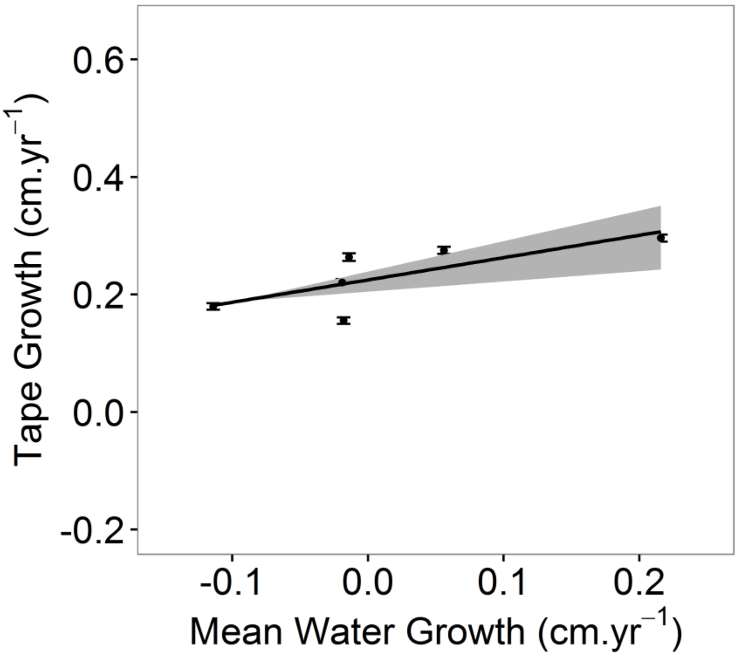


*Figure 4 revised: Regression between census-wise tape growth at the "community-level" for 50ha PSP in Mudumalai and water growth of the nine trees in the plot. Mean tape growth with 95% bootstrapped CI for growth are shown for each census-interval. Tape growth = 0.225 [0.208, 0.239] + 0.380 [0.173, 0.519] *Water Growth; p-value <0.001 for both slope and intercept. Values in brackets are 95% bootstrapped CI for intercept and slope obtained fromnon-parametric bootstrapping with 5000 replicates both water growth of the nine trees for mean growth and tree community for mean growth for each census and fitting a regression each time. This propogated error in water growth observed in nine trees in estimating mean water growth in the regression and that in estimating community mean growth.*

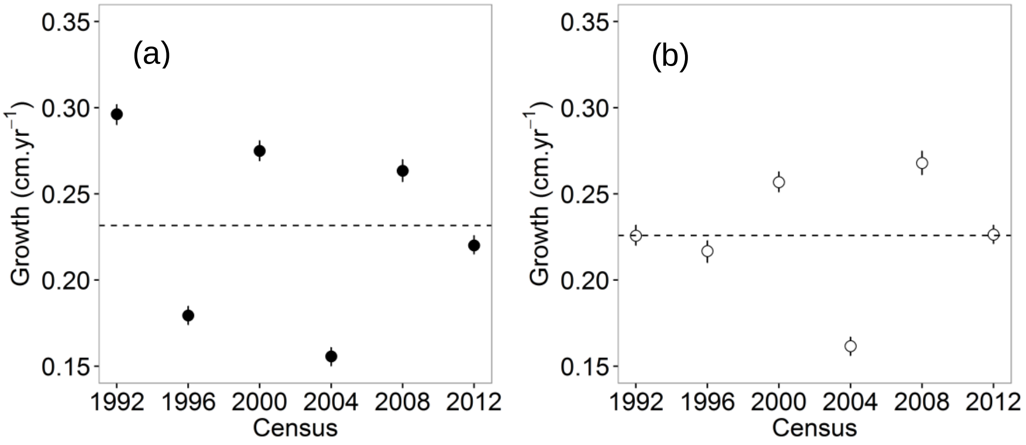


Figure 5 revised: Tape growth at "community-level" for the 50 ha MFDP (a) before and (b) after bias correction for each census. This bias correction incroporated error in the slope of the relationship between community-growth and water growth (see Figure 4 revised caption): Rather than using the mean slope for correction, for each tree a bootstrapped estimate of the slope was resampled from the 5000 estimates generated above. Mean and 95% bootstrapped CI bars are presented. Dashed line represents mean growth rate across censuses.

References

Baker, T.R., Affum-Baffoe, K., Burslem, D.F.R.P., Swaine, M.D., 2002. Phenological differences in tree water use and the timing of tropical forest inventories: conclusions from patterns of dry season diameter change. For. Ecol. Manag. 171, 261 – 274. doi:10.1016/S0378-1127(01)00787-3

Borchert, R., 1994a. Water status and development of tropical trees during seasonal drought. Trees 8, 115–125.

Borchert, R., 1994b. Soil and Stem Water Storage Determine Phenology and Distribution of Tropical Dry Forest Trees. Ecology 75, 1437–1449. doi:10.2307/1937467

Champion, H.G., Seth, S.K., 1968. A Revised Survey of the Forests Types of India.

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. doi:10.1007/s00442-005-0100-x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. n/a–n/a. doi:10.1111/gcb.12629

Clark, D.B., Kellner, J.R., 2012. Tropical forest biomass estimation and the fallacy of misplaced concreteness. J. Veg. Sci. 23, 1191–1196. doi:10.1111/j.1654-1103.2012.01471.x

Condit, R., 1998. Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer.

Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P., Foster, R.B., 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50–ha plots. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 354, 1739–1748. doi:10.1098/rstb.1999.0517

Cushman, K.C., Muller-Landau, H.C., Condit, R.S., Hubbell, S.P., 2014. Improving estimates of biomass change in buttressed trees using tree taper models. Methods Ecol. Evol. n/a–n/a. doi:10.1111/2041-210X.12187

Feeley, K.J., Joseph Wright, S., Nur Supardi, M.N., Kassim, A.R., Davies, S.J., 2007. Decelerating growth in tropical forest trees. Ecol. Lett. 10, 461–469. doi:10.1111/j.1461-0248.2007.01033.x

Holbrook, N.M., Zwieniecki, M.A., 2011. Vascular Transport in Plants. Academic Press.

Karling, J.S., 1934. Dendrograph Studies on Achras zapota in Relation to the Optimum Conditions for Tapping. Am. J. Bot. 21, 161–193. doi:10.2307/2436370

Klepper, B., Browning, V.D., Taylor, H.M., 1971. Stem Diameter in Relation to Plant Water Status. Plant Physiol. 48, 683–685. doi:10.1104/pp.48.6.683

Kozlowski, T.T., 1971. Growth and Development of Trees: Cambial growth, root growth, and reproductive growth. Academic Press.

Kozlowski, T.T., Winget, C.H., 1964. Diurnal and Seasonal Variation in Radii of Tree Stems. Ecology 45, 149–155. doi:10.2307/1937115

Maas, M., Burgos, A., 2011. Water Dynamics at the Ecosystem Level in Seasonally Dry Tropical Forests, in: Dirzo, R., Young, H.S., Mooney, H.A., Ceballos, G. (Eds.), Seasonally Dry Tropical Forests - Ecology and Conservation. Island Press.

Malhi, Y., 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. J. Ecol. 100, 65–75. doi:10.1111/j.1365-2745.2011.01916.x

Markesteijn, L., Iraipi, J., Bongers, F., Poorter, L., 2010. Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. J. Trop. Ecol. 26, 497–508. doi:10.1017/S0266467410000271

Marthews, T.R., Metcalfe, D.J., Malhi, Y., Huaraca, H.W., Riutta, T., Ruiz-Jaen, M., Girardin, C.A.J., Butt, N., Cain, R., Oliveras, M.I., and colleagues from the RAINFOR and GEM networks, 2012. Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field Manual for Intensive Census Plots (v2.2). (Manual).

Meinzer, F.C., Andrade, J.L., Goldstein, G., Holbrook, N.M., Cavelier, J., Wright, S.J., 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. Oecologia 121, 293–301. doi:10.1007/s004420050931

Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.E., Hart, T., Hubbell, S.P., Itoh, A., Kassim, A.R., LaFrankie, J.V., Lee, H.S., Losos, E., Makana, J.-R., Ohkubo, T., Sukumar, R., Sun, I.-F., Nur Supardi, M.N., Tan, S., Thompson, J., Valencia, R., Muñoz, G.V., Wills, C., Yamakura, T., Chuyong, G., Dattaraja, H.S., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S., Suresh, H.S., Thomas, D., Vallejo, M.I., Ashton, P., 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol. Lett. 9, 575–588. doi:10.1111/j.1461-0248.2006.00904.x

Muller-Landau, H.C., Detto, M., Chisholm, R.A., Hubbell, S.P., Condit, R., 2014. Detecting and projecting changes in forest biomass from plot data, in: Forests and Global Change, Ecological Reviews. Cambridge University Press.

Murali, K.S., Sukumar, R., 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. Oecologia 94, 114–119. doi:10.1007/BF00317311

Nath, C.D., Dattaraja, H.S., Suresh, H.S., Joshi, N.V., Sukumar, R., 2006. Patterns of tree growth in relation to environmental variability in the tropical dry deciduous forest at Mudumalai, southern India. J. Biosci. 31, 651–669. doi:10.1007/BF02708418

Pélissier, R., Pascal, J.., 2000. Two-year tree growth patterns investigated from monthly girth records using dendrometer bands in a wet evergreen forest in India. J. Trop. Ecol. 16, 429–446. doi:10.1017/S0266467400001498

Prasad, S.N., Hegde, M., 1986. Phenology and seasonality in the tropical deciduous forest of Bandipur, South India. Proc. Indian Acad. Sci. Plant Sci. 96, 121–133. doi:10.1007/BF03053328

Puri, G.S., 1960. Indian Forest Ecology: A Comprehensive Survey of Vegetation and Its Environment in the Indian Subcontinent. Oxford University Press, New Delhi.

Rao, K.S., Dave, Y.S., 1981. Seasonal variations in the cambial anatomy of Tectona grandis (Verbenaceae). Nord. J. Bot. 1, 535–542. doi:10.1111/j.1756-1051.1981.tb00719.x

R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Australia.

Ruiz, L., Varma, M.R.R., Kumar, M.S.M., Sekhar, M., Maréchal, J.-C., Descloitres, M., Riotte, J., Kumar, S., Kumar, C., Braun, J.-J., 2010. Water balance modelling in a tropical watershed under deciduous forest (Mule Hole, India): Regolith matric storage buffers the groundwater recharge process. J. Hydrol. 380, 460–472. doi:10.1016/j.jhydrol.2009.11.020

Scholz, F.C., Bucci, S.J., Goldstein, G., Meinzer, F.C., Franco, A.C., Miralles-Wilhelm, F., 2008. Temporal dynamics of stem expansion and contraction in savanna trees: withdrawal and recharge of stored water. Tree Physiol. 28, 469–480. doi:10.1093/treephys/28.3.469

Sheil, D., 1995. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. For. Ecol. Manag. 77, 11 – 34. doi:DOI: 10.1016/0378-1127(95)03583-V

Sheil, D., 1997. Long-term growth and rainfall in a Ugandan moist forest: seasonal rhythms and flexing stems. Commonw. For. Rev. 76, 121–127.

Sheil, D., 2003. Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by dendrometer bands. Can. J. For. Res. 33, 2027–2035. doi:10.1139/x03-121

Sukumar, R., Dattaraja, H.S., Suresh, H.S., Radhakrishnan, J., Vasudeva, R., Nirmala, S., Joshi, N.V., 1992. Long term monitering of vegetation in a tropical deciduous forest in Mudumalai, southern India. Curr. Sci. 62, 608–616.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Joshi, N.V., 1998. Dynamics of a tropical deciduous forest: population changes (1988 through 1993) in a 50-ha plot at Mudumalai, southern India.

Sukumar, R., Suresh, H.S., Dattaraj, H.S., John, R., Joshi, N.V., 2004. Mudumalai forest dynamics plot, India, in: Tropical Forest Diversity and Dynamics: Findings from a Large-Scale Plot Network. University of Chicago Press, Chicago, pp. 551–563.

Suresh, H.S., Dattaraja, H.S., Mondal, N., Sukumar, R., 2013. Seasonally Dry Tropical Forests in Southern India: An Analysis of Floristic Composition, Structure, and Dynamics in Mudumalai Wildlife Sanctuary, in: McShea, W.J., Davies, S.J., Bhumakphan, N. (Eds.), The Ecology and Conservation of Seasonally Dry Forests in Asia. Smithsonian Institution Scholarly Press, Washington, D.C.

Suresh, H.S., Dattaraja, H.S., Sukumar, R., 2010. Relationship between annual rainfall and tree mortality in a tropical dry forest: Results of a 19-year study at Mudumalai, southern India. For. Ecol. Manag. 259, 762–769.

Suresh, H.S., Sukumar, R., 2009. Influence of climatic variability on Tree phenology in the Tropical Dry forests of Mudumalai, southern India, in: Diloksumpun, S., Puangchit, L. (Eds.), Dry Forest Ecology and Conservation. Vol. 5. Tropical Forestry Change in a Changing World. FORTROP II. International Conference. Presented at the Tropical Forestry Change in a Changing world. FORTROP II. International Conference., Bangkok, Thailand.

Talbot, J., Lewis, S.L., Lopez-Gonzalez, G., Brienen, R.J.W., Monteagudo, A., Baker, T.R., Feldpausch, T.R., Malhi, Y., Vanderwel, M., Araujo Murakami, A., Arroyo, L.P., Chao, K.-J., Erwin, T., van der Heijden, G., Keeling, H., Killeen, T., Neill, D., Núñez Vargas, P., Parada Gutierrez, G.A., Pitman, N., Quesada, C.A., Silveira, M., Stropp, J., Phillips, O.L., 2014. Methods to estimate aboveground wood productivity from long-term forest inventory plots. For. Ecol. Manag. 320, 30–38. doi:10.1016/j.foreco.2014.02.021

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., Bongers, F., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J. Ecol. 99, 254–264. doi:10.1111/j.1365-2745.2010.01741.x

Wagner, F., Rossi, V., Aubry-Kientz, M., Bonal, D., Dalitz, H., Gliniars, R., Stahl, C., Trabucco, A., Hérault, B., 2014. Pan-Tropical Analysis of Climate Effects on Seasonal Tree Growth. PLoS ONE 9, e92337. doi:10.1371/journal.pone.0092337

Zweifel, R., Häsler, R., 2001. Dynamics of water storage in mature subalpine Picea abies: temporal and spatial patterns of change in stem radius. Tree Physiol. 21, 561–569. doi:10.1093/treephys/21.9.561

Chapter 5

Hydrostatic bias and size-dependency in tree growth rates change along a precipitation gradient in a seasonally dry tropical forest

A partial version of this chapter is in review with *Environmental Research Letters*.

Abstract

Understanding tree diameter growth along a spatial climatic gradient is important to modeling species distributions, ecosystem properties and carbon fluxes under climate change. However, a series of confounding factors make a straightforward use of 'space for time' substitution modeling difficult.

In this study, we used dendrometer-based annual growth estimates of trees measured over three successive years in permanent sampling plots (PSPs) along a precipitation gradient in southern India that spans a tropical dry deciduous forest/mesic savanna to moist deciduous forest transition. Along this gradient, we evaluated shifts in two key confounding factors, namely, bias due to water-induced fluctuations and growth – diameter allometry. We adapted a previously described method to estimate and correct for hydrostatic bias in mean tree community growth rates. To evaluate shift in allometry along this precipitation gradient we tested the effect and interaction of tree diameter and plot mean annual precipitation on growth. We also evaluated the effect of species identity on this shift using linear mixed effects models.

We report three main results: (i) The extent of bias decreased from dry to moist forest and notably influenced estimated yearly growth – climate relationships. (ii) A significant shift in growth – diameter relationship was observed along the gradient, revealing that the increase in growth along the gradient was mainly due to large trees. Given that large trees play a disproportionately greater role in the carbon cycling by vegetation, this result has potentially strong implications for modeling biomass flux and carbon sequestration under climate change. (iii) The observed pattern of small trees growing faster in dry forest was mostly explained by species identity, which is pertinent for modeling community dynamics under climate change, including savanna – forest biome shifts.

Introduction

Climatic gradients in space are widely used to identify relationships between forest ecosystem properties and climatic conditions. These relationships are often used to infer forest response to climate change over time, which is important given the substantial contribution of forests to the global carbon cycle (Bonan, 2008; Grace et al., 2006) and to other ecosystem services (Hassan et al., 2005). However, a variety of confounding factors make a straightforward use of the 'space for time' approach difficult, for example, long-term adaptation to local climatic conditions, species turnover (Dunne et al., 2004; Rapp et al., 2012).

How tree diameter growth responds to variability and change in water availability is fundamental to our understanding of species distributions and predicting impact of climate change on forest carbon fluxes. This is because water availability is the strongest environmental determinant of species richness (Davidar et al., 2005; Gentry, 1988; Poorter et al., 2004; ter Steege et al., 2006), composition (Bongers et al., 2004; Davidar et al., 2007; Hall and Swaine, 1976), distribution (Baltzer et al., 2008; Comita and Engelbrecht, 2014; Engelbrecht et al., 2007; Toledo et al., 2012), and tree growth and productivity (Becknell et al., 2012; Schuur, 2003; Toledo et al., 2011), especially in tropical forests, which are rich in biodiversity (Dirzo and Raven, 2003) and play a disproportionate role in the global carbon and energy cycle (Bonan, 2008).

As a consequence of anthropogenic greenhouse gas emissions, increasing atmospheric and sea-surface temperatures are predicted to cause large shifts in precipitation patterns in the tropics, although projections vary widely among regions and significant increases or decreases in annual precipitation and dry season length are being predicted (Hulme and Viner, 1998; IPCC, 2014; Neelin et al., 2006). Precipitation changes in the tropics have been highly spatially variable, although a sharp decline in annual precipitation, along with increases in dry season length, intensity and variability in precipitation, is already being witnessed in the north African and Asian tropics in the recent past (Goswami et al., 2006; Malhi and Wright, 2004; Roxy et al., 2015). In addition, large scale deforestation and fragmentation is likely to exacerbate drying conditions (Hoffmann et al., 2003; Malhi et al., 2008; van der Werf et al., 2008).

Studies assessing tropical tree growth response to climatic variables are limited and sometimes contradictory (Baker et al., 2004; Clark and Clark, 2011; Clark et al., 2010; Feeley et al., 2007; Lewis et al., 2009; Phillips et al., 1998; Wright, 2005). Given that multiple climatic and other environmental factors co-vary and influence tree growth in time, disentangling effect of one factor is challenging, especially given that long time-series data are scarce for the tropics. Although models usually predict that the response of carbon balance of the forest to drying and warming conditions would cause a positive feedback to global warming, large uncertainties remain (Berthelot et al., 2005; Cox et al., 2000; IPCC, 2014; Matthews et al., 2007).

Spatial climatic gradients are used to complement these data deficiencies. However, along these gradients, several abiotic and biotic factors such as precipitation, nutrient availability, fire frequency, species composition, often co-vary. Some of these variations are increasingly accounted for in climate gradient studies; for example, Rapp et al. (2012) included the effect of species compositional change while assessing growth trend along a temperature gradient. Some other variations are usually under appreciated. For example, tree size distribution and growth – diameter allometric relationship itself could change with the gradient, which is important as growth rates are size dependent: comparing three tropical forest sites along a 2000-3000 mm MAP precipitation gradient in Panama, Condit et al. (2004) found that saplings have faster growth rates, while large trees have slower growth rates in drier compared to intermediate or wetter site. These differences were also reflected by individual species. Authors suggested that the slow growth rate of large trees in drier forests is due to longer annual dry season and deciduousness, while faster growth rate of juveniles in drier forests due to greater light penetration to the forest floor. In a study of growth – diameter allometric relationship across dry and wet tropical forests around the globe, Muller-Landeau et al. (2006) also found faster growth rates in small individuals in dry compared to moist tropical forests. This was attributed to the open-canopied structure and reduced competition for resources, as a consequence of low-densities of large trees. Species turnover and adaptive differences could have also contributed to this pattern, given that high sapling growth rate is also known to be the 'fire trap' escape strategy in savanna tree species (Bond et al., 2012).

The frequency at which tree diameter growth is measured is important in both spatial gradient and temporal studies (Sheil, 1995). Multi-annual frequency is not only a mix of high and low precipitation years but, at this frequency variability in other environmental factors, such as fire and storms, could also affect tree growth, or cause substantial tree turnover in numbers and species composition (Sheil, 1995).

Thus to better capture precipitation-specific signal and minimize variability in other factors, it is important to measure growth at a time scale, typically the annual scale, at which precipitation varies the most at the given site. This scale also allows us to incorporate adequate climatic variability needed to assess climate sensitivity in tree growth (Clark and Clark, 2011).

However, there are several methodological constraints in these measurements. For example, graduated tapes or calipers normally employed in permanent sampling plots, allow us to measure a large number of trees though with poor accuracy, but are generally not suitable at short time scales. Band dendrometers, given their higher precision and accuracy (Clark et al., 2007), allow measurement of tree diameter growth at annual and sub-annual scale and are being increasingly used for this purpose.

Measurement bias could also vary along the gradient. The correction of bias in temporal growth estimates due to stem shrinkage and expansion due to water-induced fluctuations is critical in understanding growth – water availability relationships (Chitra-Tarak et al., 2015). This could be relevant for spatial gradient relationships as well. If a drought year affects water availability in the drier sites more severely than in the moister sites of the gradient, larger differences in the water-status would lead to greater bias in measurements for trees in the former than in the latter. Compared to multi-annual scale, this bias is likely to be higher at annual intervals; this is because at the annual scale the diameter increment due to woody growth is relatively small compared to the bias due to hydrostatic stem fluctuations and measurement error (Sheil, 2003, 1995). A method for correcting this hydrostatic bias was proposed by Chitra-Tarak et al. (2015). The authors found that the hydrostatic bias measured in the growth time series of a few trees also reflected in the growth time series at the whole community level to a certain but significant extent, and was corrected to that extent. The factors responsible for such hydrostatic and other kinds of measurement bias could also vary along the gradient, including size and species-specific properties such as bark thickness, stem damage due to fire or mammalian herbivory, occurrence of buttresses (Cushman et al., 2014) and timing of phenological events (Sheil, 1995).

In this study, we evaluated key confounding factors in growth – precipitation gradient analysis using dendrometer based annual growth estimates of trees in permanent sampling plots (PSPs) along a distinct precipitation gradient in southern India. We adapted a novel method (Chitra-Tarak et al., 2015) that uses stem hydrostatic bias measured in a few trees at the center of this gradient and examined whether this could be used to estimate and correct for bias in annual diameter growth records of PSPs across the spatial precipitation gradient measured over three successive years. We then evaluated tree growth relationships along this spatial precipitation gradient spanning a tropical dry deciduous forest to moist deciduous forest transition, and specifically examined if and how tree growth estimates along this gradient were influenced by (i) shift in the extent of stem hydrostatic bias, (ii) shift in growth – diameter allometric relationship, and (iii) species turnover along the gradient.

Materials & Methods

The Study Area

We collected tree growth data from seven 1-ha permanent sampling plots (PSPs) in Mudumalai Wildlife Sanctuary and National Park, southern India, (hereafter Mudumalai) established along a distinct precipitation gradient in the rain shadow of the Western Ghats and from one 50-ha PSP situated at the centre of the gradient (Table 1, Figure 1). The 50-ha PSP (the Mudumalai Forest Dynamics Plot or MFDP), was established in 1988-1989 (Sukumar et al. 1992, 1988), while the seven 1-ha plots were established in 1994 (Suresh et al., 2011) for monitoring long-term forest dynamics according to the protocols of the CTFS-ForestGEO Network (Anderson-Teixeira et al., 2015; Condit, 1998), with each stem above 10 mm DBH (Diameter at Breast Height; 130 cm from ground) given a unique number, mapped on a 10 m x 10 m grid and identified to species (or morpho - species) level. Across the 40 km east-west spread of Mudumalai, mean annual precipitation (MAP) varies from 700 mm in the east to 1700 mm in the west (Dattaraja et al., 2013), primarily due to the South-West (summer) monsoon that brings ~70% of the annual precipitation between June-September. The

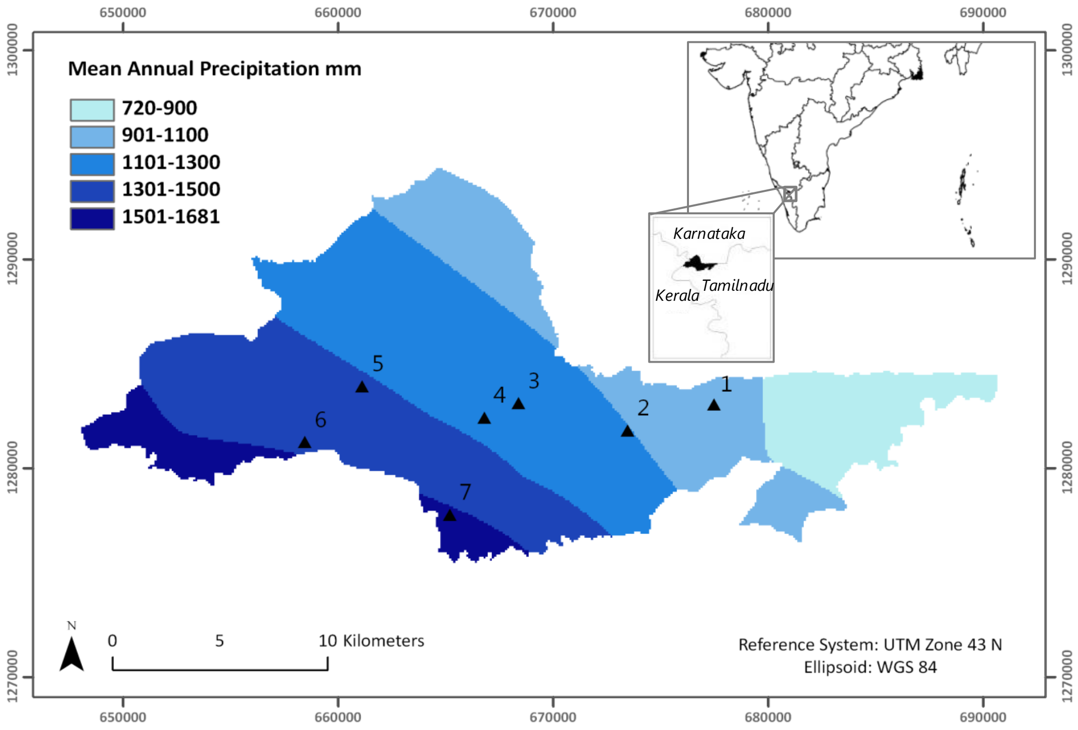


Figure 1: An interpolation map depicting the precipitation gradient in Mudumalai Wildlife Sanctuary, southern India, adapted from (Dattaraja et al., 2013). The seven permanent forest dynamics plots included in this analysis are shown. Trees on which bias is measured are from plot 4, which is a subsection of the Mudumalai 50-ha MFDP. Inset illustrates location of Mudumalai in the context of peninsular Indian states.

eastern part of Mudumalai also receives rains from the returning North-East (winter) monsoon during October-December. Mean annual precipitation (MAP) for each plot was obtained from an interpolation map using 1990-2010 monthly precipitation records from 16 rain-gauge stations in and around Mudumalai (Dattaraja et al., 2013). The direction of the gradient remains stable across years, despite the inter-annual variation in precipitation. For the study period, precipitation during 2012 was 30% less than the long-term average (1988-2013), whereas during 2011 and 2013 it was close to it.

*Table 1: Location, mean annual rainfall, forest type, species richness and tree density of each of the seven 1ha PSPs in Mudumalai included in this study. * MAP = Mean Annual Precipitation (Dattaraja et al., 2013). ** Dry = Tropical Dry Deciduous Forest/Tropical Mesic Savanna, Moist = Tropical Moist Deciduous Forest. *** For stems >= 1 cm DBH/ha in 2007.*

Plot No.	Plot Location	Latitude (°N)	Longitude (°E)	MAP (mm)*	Forest Type**	Species Richness***	Tree Density***
1	Bare	11.60202	76.62773	963.4	Dry	20	516
2	Circular Rd	11.59086	76.59089	1107.1	Dry	11	215
3	K.M. Road	11.60289	76.54455	1197.3	Dry	30	510
4	50 ha	11.59679	76.52985	1250.7	Dry	18	229
5	Munde Moole	11.61061	76.47785	1324.9	Moist	35	559
6	Church Road	11.58654	76.45324	1472.4	Moist	43	555
7	Thorapalli	11.55478	76.51495	1529.8	Moist	45	406

Across the sanctuary altitude ranges from 300-1200 m asl, but most of the region lies at 900-1000 m asl. The temperature regime is relatively constant along the precipitation gradient: for example, mean monthly $T_{max,}$ T_{min} are, respectively, 27.8°C, 16.8°C in the east and 27.7°C, 18.3°C at the center of the gradient. Given this precipitation and temperature regime, with 6-8 dry months (precipitation less than 100 mm), and annual potential evapotranspiration to precipitation ratio being less than 1.0, the entire Mudumalai could be classified as a seasonally dry tropical forest (Murphy and Lugo, 1986; Suresh et al., 2011). Along the precipitation gradient vegetation changes from tropical dry thorn and deciduous forest in the east to tropical moist deciduous forest interspersed with swampy grasslands and semi-evergreen forest patches in the west (Sharma et al., 1977; Suresh et al., 2011). The seven chosen PSPs lie in the precipitation range of 960mm to 1530 mm MAP. Hereafter, plots 1-4 will be grouped as dry forest plots and plots 5-7 as moist forest plots, although they lie on a continuum of tropical dry and moist deciduous forest gradient. While the tropical moist deciduous forest here is a closed canopied forest, the tropical dry deciduous forest may also be termed as tropical mesic savanna (Ratnam et al., 2011), given their distinguishing characters, such as the open canopied, open-crown structure with a high-light understory, dominance of C_4 grasses, frequent ground fires and post-fire recovery through resprouts, with root-suckering being the common reproductive strategy (Sukumar et al., 2005; Suresh et al., 2011).

Tree growth and bias in measurements

In each of the seven PSPs mentioned above (see Suresh et al. 2011 for greater details of these PSPs), home-made steel band dendrometers (following the CTFS protocol, http://www.ctfs.si.edu/data///documents/Metal_Band_Dendrometer_Protocol_20100330.pdf) were installed (10 cm above DBH) during 2009-2010 on all trees across species above 5-cm DBH in five randomly selected 20m x 20m quadrats, i.e. 20% area of the 1-ha plot (by a random draw of five quadrats out of the 26 quadrats in the 40m x 260m plot) (Table 2). Additionally, bands were installed on trees in other quadrats of the plot to increase samples sizes for less common species (to at least 7 individuals, if present—again by a random draw if the numbers were greater than 7). These together totaled to 836 trees from 73 species in seven plots (Table 2).

Table 2: Details of number of trees and species with dendrometer bands installed at each of the seven PSPs in this study, with dates of dendrometer installation and measurements for calculating annual growth rates.

Plot No.	Plot Location	No. of trees	No. of Species	Dendrometer Installation Dates	Annual Dendrometer Measurement Date			
					2011	2012	2013	2014
1	Bare	125	19	25 -27 Apr 2009	25 Mar	09 Mar	25 Jan	28 Feb
2	Circular Rd	74	9	21 May 2009	15 Mar	23 Feb	12 Jan	12 Feb
3	K.M. Road	100	17	18 Jan 2010	14 Mar	22 Feb	11 Jan	18 Feb
4	50 ha	94	14	21 - 22 Apr 2009	12 Mar	17 Feb	09 Jan	24 Feb
5	Munde	116	30	15 May - 9 Jun 2009	16 Mar	18 Feb	16 Jan	04 Mar
6	Church	127	32	8 May - 13 Jun 2009	19 Mar	10 Mar	17 Jan	21 Feb
7	Thorapalli	152	33	15 - 25 Jul 2009	17 Mar	07 Mar	18 Jan	20 Feb

Dendrometer measurements were taken almost every other month from August 2009 through November 2011, and then during the dry season of three successive years (2012, 2013, 2014; see Table 3) using a digital caliper (0.01 mm resolution). For evaluating differences across the rainfall gradient in seasonal stem shrinkage and expansion, dendrometer measurements from Aug 2009 through Feb 2012 were used. For estimating annual growth, dry season dendrometer measurements from 2011 through 2014 were used (Mar 2011, Feb-Mar 2012, Jan 2013 and Feb 2014; see Table 2), the period for which data for all the seven plots were available.

For each successive interval, diameter growth for each tree was calculated as change in diameter at the height where dendrometers were installed (140 cm from the ground). While the initial diameter was measured using a graduated tape with 1 mm resolution, successive diameters were calculated by iteratively optimizing the following equation (http://richardcondit.org/data/dendrometer/calculation/Dendrometer.php):

$$D_{t+1} = D_t - \arcsin(C_t/D_t) \times D_t/\pi + \arcsin(C_{t+1}/D_{t+1}) \times D_{t+1}/\pi$$

Where, C_t, C_{t+1} are the successive chords on the tree circumference measured by the dendrometers (at 0.01 mm resolution) and D_t, D_{t+1} the diameters at time t and t+1.

For assessing variation in seasonal stem diameter fluctuations along the gradient, we compared across plots community-wide average trends in cumulative diameter increment (Aug 2009 - Feb-Mar 2012) (Figure 2a), and mean of community-wide wet-to-dry season stem diameter change during these three years (Oct-Nov 2009-to-Mar 2010, Nov 2010-to-Mar 2011, Nov 2011-to-Mar 2012; Figure 2b). Due to lack of seasonal data in the following years, we could not compare extent of seasonal variations for the exact years for which annual growth rates were calculated (Mar 2011-to-Mar 2012, Mar 2012-to-Jan 2013, Jan-2013-to-Feb-Mar-2014). For each tree change in diameter was calculated at annual scale, which was termed as 'Dendrometer Growth'. Given that the majority of trees are deciduous during the dry season when cambium likely remains dormant (Rao and Dave, 1981), annual growth measurement in the dry season ensured that growth in the corresponding monsoonal year, viz. 2011, 2012 & 2013 respectively, was complete. We also calculated mean annual Dendrometer Growth for each tree by taking the average of these three years of growth (cm.year^{-1}), which is hereafter referred to as 3-year mean growth. At one of the above-mentioned one-ha plots (Table 2, plot number 4, a part of the 50-ha plot (MFDP) (Sukumar et al., 1992; Suresh et al., 2011) located at the center of the precipitation gradient, trees which were part of the Dendrometer based growth census mentioned-above were chosen to measure bias due to water-induced fluctuations. As the direction of the precipitation gradient remains stable across years, we assumed that tree water-status should vary in the same direction across years in all plots. Thus water-induced fluctuations measured at the center of the gradient should reflect the direction of these fluctuations for other plots along the gradient. For example, a positive bias measured in the center will remain positive or null in the other plots, although their amplitude may vary.

From these, three trees of Tectona grandis L. f., a species that shows distinct, identifiable annual rings and is commonly used for dendro-climatalogical studies in the tropics (Priya and Bhat, 1998; Pumijumnong, 2013; Rao and Dave, 1981) were chosen to measure woody diameter growth, hereafter referred to as 'Ring Growth', based on tree ring widths. For this, in November 2013, from each tree, increment cores (0.5 cm

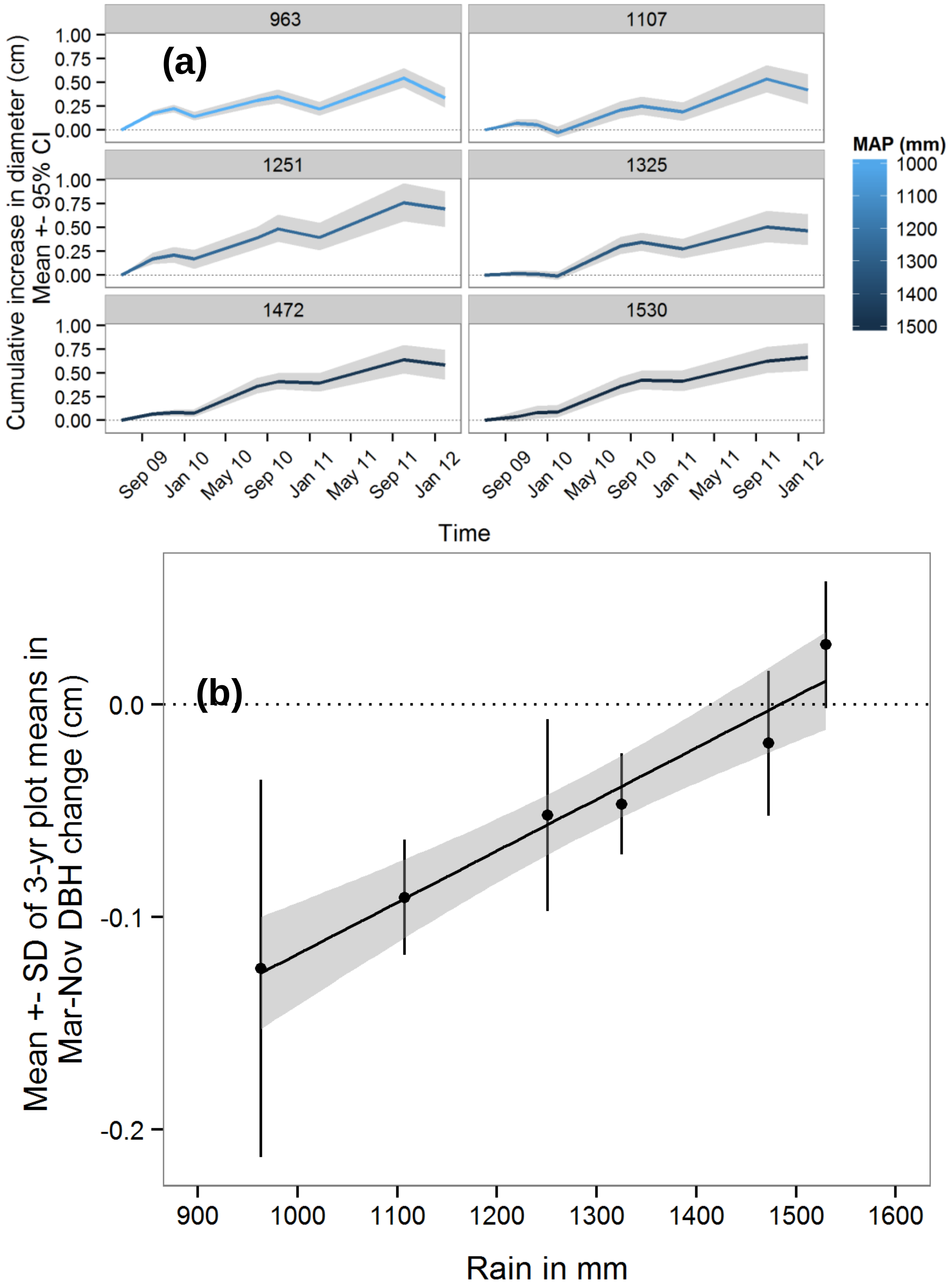


Figure 2: Seasonal variation in stem expansion and shrinkage at plots along the rainfall gradient (Number headings are plot mean annual rainfall in mm). (a) Community-wide mean cumulative diameter at the sevel plot locations. Panel headings denote plot number (with plot MAP in mm). Grey envelopes denote 95% bootstrapped confidence intervals. (b) Mean (+-SD) of Community-wide mean wet-to-dry season change across three years (Oct-Nov 2009- Mar 2010, Nov 2010-Mar 2011, Nov 2011-Mar 2012) versus plot MAP.

Table 3: Dates for seasonal dendrometer measurements.

Plot No.	Plot site	Aug'09	Oct-Nov'09	Dec'10-Jan'11	Mar'10	May'10	Jul'10	Sep'10	Nov'10	Jan'11	Mar'11	May-Jun'11	Jul-Aug'11	Nov'11	Mar'12	Jan'13	Feb-Mar'14
1	Bare	08 Aug	28 Oct	12 Jan	20 Mar	19 May	21 Jul	19 Sep	27 Nov	19 Jan	25 Mar	01 Jun	16 Aug	30 Nov	09 Mar	25 Jan	28 Feb
2	Circular Rd	01 Aug	27 Oct	23 Dec	10 Mar	06 May	29 Jul	15 Sep	13 Nov	17 Jan	15 Mar	18 May	01 Aug	25 Nov	23 Feb	12 Jan	12 Feb
3	K.M. Road	NA	NA	18 Jan	11 Mar	11 May	13 Jul	13 Sep	15 Nov	07 Jan	14 Mar	19 May	16 Jul	21 Nov	22 Feb	11 Jan	18 Feb
4	50 ha	05 Aug	20 Oct	07 Jan	07 Mar	10 May	15 Jul	14 Sep	18 Nov	10 Jan	12 Mar	17 May	15 Jul	19 Nov	17 Feb	09 Jan	24 Feb
5	Munde Moole	04 Aug	30 Oct	24 Dec	09 Mar	07 May	16 Jul	16 Sep	20 Nov	12 Jan	16 Mar	19 May	29 Jul	22 Nov	18 Feb	16 Jan	04 Mar
6	Church Road	NA	23 Oct	26 Dec	17 Mar	12 May	23 Jul	20 Sep	22 Nov	13 Jan	17 Mar	28 May	26 Jul	24 Nov	07 Mar	18 Jan	20 Feb
7	Thorapalli	03 Aug	05 Nov	25 Dec	13 Mar	08 May	17 Jul	17 Sep	16 Nov	08 Jan	19 Mar	20 May	12 Aug	18 Nov	10 Mar	17 Jan	21 Feb

diameter, 10 cm long) were collected in 3-5 radial directions at 125 cm from ground. For each tree, annual rings were identified for year 2011, 2012 and 2013 and ring widths were measured, converted to diameter, pooled by year across all core samples, and a mean was taken as Ring Growth for that given year. Bias was calculated for each year as the difference between Dendrometer Growth and Ring Growth. This was termed as 'Water Growth', as proposed by Chitra-Tarak et al. (2015), since the bias was most likely due to water-induced fluctuations for each tree, although other causes such as bark loss or stem damage cannot be ruled out.

We investigated growth-diameter relationship and shift therein along the rainfall gradient using the above-mentioned dendrometer-based diameter census datasets at the seven 1-ha plots (about 100-200 trees per plot). We also made use of the larger tape-based diameter census dataset from the 50-ha plot (MFDP) situated at the center of the rainfall gradient to more closely examine this relationship for a tropical dry deciduous forest/mesic savanna. We also evaluated whether the relationship was consistently found across census intervals. For this we selected only single-stemmed trees greater than 1cm DBH independently present in two successive 4-year scale census intervals from 1988-2012, amounting to 10088 to 16484 trees depending on census. Growth rates less than -0.5 $cm.yr^{-1}$ and greater than 1.5 $cm.yr^{-1}$ were treated as erroneous and removed. We then visually examined growth-diameter plots at the log-log scale for each census interval.

Statistical Approach

Bias due to water-induced fluctuations

Annual Water Growth for the three trees was examined for the three successive years and significant variation was found across years (Figure 3a). Most of the variation in Dendrometer Growth of these trees across three years was explained by Water Growth (R^2 = 0.93, Figure 3b).

To test whether mean annual Water Growth in these three trees could be used as a proxy for mean annual Water Growth in tree communities across the precipitation gradient, for each plot along the gradient we regressed annual Dendrometer Growth rates for all trees in the given plot against the annual mean Water Growth measured in the three trees. Water Growth is the bias most likely due to difference in water-status of the tree at the time of successive measurement occasions and is affected by instantaneous water-availability, whereas woody growth is affected by water availability throughout the census interval.

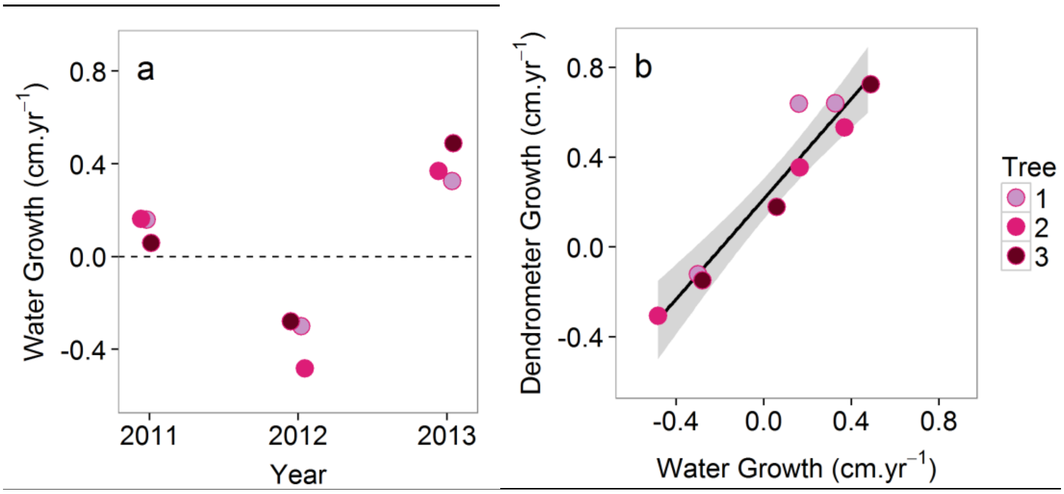


Figure 3: Water Growth (bias due to water-induced fluctuations) in the three trees (a) across three years, and regressed (b) against the Denrometer Growth in the three trees. Gray envelope shows 95% confidence interval.

Water Growth is then expected to be largely independent of woody growth. Indeed Chitra-Tarak et al. (2015) found that Water Growth and Ring Growth were largely independent in a tape–based growth measurement study. The regression slope for each plot can thus be taken as indicative of bias due to water-induced fluctuations and used to correct the bias at the mean community level of the plot (Chitra-Tarak et al., 2015). For cases in which the slope of the relationship was significantly different from zero, we subtracted the slope effect of the mean Water Growth of the three trees from the Dendrometer Growth for each tree to correct mean bias and to estimate woody growth in the given year (Chitra-Tarak et al., 2015). Note that this method is valid for correcting bias at mean plot level, but should not be used to interpret individual trees, as bias may vary with individual trees according to size, species, and location. To estimate the impact of hydrostatic bias, we used yearly Dendrometer Growth for all trees and compared growth–MAP linear relationships across years, before and after bias correction. We also evaluated bias-uncorrected and corrected 3-yearly mean tree growth rates–MAP linear relationship. Note that this comparison is based on our method of bias correction that affects only the mean and not the standard deviation of plot level growth rates. Although bias certainly varies among trees according to sizes, species, and other factors, the impact of this on standard deviation is difficult to predict (in fact, it depends on the co-variation between actual woody growth and extent of bias for each size class, species, etc.). Hence, the significance of the difference in the relationships above should be interpreted with caution.

Modeling growth along the gradient

For the following analysis, we did not use bias-corrected Dendrometer Growth. As mentioned earlier, the method for bias-correction, though valid for correcting bias at mean community level, is not yet fully tested and developed at the individual tree level for any potential size-and species-dependency in bias. We used the bias-uncorrected, 3-year mean growth rates for each tree (that will be referred to as growth), since this interval is likely to be only marginally affected by bias resulting from the tree water-status being similar at the beginning and end of the 3-year interval (see Results section). We modeled growth_i as a linear function of either MAP (M1), MAP and initial DBH (diameter at breast height) (M2), or additionally with MAP and initial DBH with an interaction term (M3):

$$\text{Growth}_i = \beta_0 + \beta_1 \text{MAP}_i + \varepsilon_i \qquad \text{(M1)}$$

$$\text{Growth}_i = \beta_0 + \beta_1 \text{MAP}_i + \beta_2 \text{DBH}_i + \varepsilon_i \qquad \text{(M2)}$$

$$\text{Growth}_i = \beta_0 + \beta_1 \text{MAP}_i + \beta_2 \text{DBH}_i + \beta_3 \text{MAP}_i \text{x} \text{DBH}_i + \varepsilon_i \qquad \text{(M3)}$$

with $\varepsilon_i \sim N(0, \sigma^2)$. We centered and scaled all the fixed effect terms before model fitting. MAPxDBH was centered and scaled after multiplication.

Presence of a growth – DBH shift along the gradient, if any, should be reflected by the significance of adding an interaction term between MAP and DBH to the additive model (M2).

To evaluate the effect of species (and turnover therein) on these relationships, we also fitted Linear Mixed effects Models (LMMs) with a random intercept for species corresponding to the above three models:

$$\text{Growth}_{is} = \beta_0 + \beta_1 \text{MAP}_{is} + b_s + \varepsilon_{is} \qquad \text{(M4)}$$

$$\text{Growth}_{is} = \beta_0 + \beta_1 \text{MAP}_{is} + \beta_2 \text{DBH}_{is} + b_s + \varepsilon_{is} \qquad \text{(M5)}$$

$$\text{Growth}_{is} = \beta_0 + \beta_1 \text{MAP}_{is} + \beta_2 \text{DBH}_{is} + \beta_3 \text{MAP}_{is} \text{x} \text{DBH}_{is} + b_s + \varepsilon_{is} \qquad \text{M6)}$$

with $\varepsilon_{is} \sim N(0, \sigma^2 I)$ and $b_s \sim N(0, \tau_s^2)$. The random effects b_s for each species and the within-species error ε_{is} are assumed to be independent for different species and independent of each other for the same species. We centered and scaled all the fixed effect terms before model fitting. MAPxDBH was centered and scaled after multiplication.

To assess model performance with respect to tree size, goodness-of-fit statistics (R^2) were calculated using observed and expected growth rates of individual trees, separately for small [5-20) cm DBH and large [20-80] cm DBH trees.

Models M1-M6 were compared based on Akaike's Information Criterion (AIC) and R^2. Significance of each additional fixed-effect term in the linear regressions was tested by F tests. Significance of each additional fixed-effect term in the LMMs was tested by Chi-sq tests between successively nested models, and by AIC values that used maximum likelihood (ML) estimation. However, the final models are presented using restricted maximum likelihood (REML) estimation (Zuur et al., 2009). AIC represents a combined measure of the fit of the model based on likelihood and the penalty for complexity of the model due to the number of parameters. AIC was calculated as 2*k – 2*Log Likelihood, where k is the number of parameters. For M1, M2 and M3, k was 2, 3 and 4 respectively. For LMMs it was counted as the number of fixed effects (2, 3 and 4, for models M4, M5 and M6, respectively), plus one parameter for the species random effect for the intercept, and an additional parameter for the residual variance. Thus k was 4, 5 and 6, for model M4, M5 and M6 respectively.

All analyses were done in R statistical environment, version 3.0.2 (R Core Team, 2013). We used lme4 package for fitting LMMs, and calculating corresponding AICs and R^2. Package ggplot2 was used for graphics.

Results

Reduced seasonal hydrostatic stem-flexing with increasing plot mean annual precipitation

The community-wide mean cumulative diameter increment curves from August 2009 through March 2012 for dry forest plots showed periodic and reversible stem shrinkage—a characteristic sign of hydrostatic stem fluctuations. Cumulative diameter curves for moist forest plots were relatively non-decreasing (Figure 2a). Community-wide mean wet-to-dry season stem shrinkage during these three years indeed systematically and significantly decreased with plot MAP ($R^2 = 0.95$, $P < 0.001$; Figure 2b). This suggests that annual growth estimation in drier plots is likely to be more affected by bias due to hydrostatic stem-flexing than wetter plots. Absence of reversible stem-shrinkage in the moister plots, however, does not obliterate the possibility that at the moist forest plots, with greater proportion of evergreen and brevi-deciduous species (unpublished data, R.C.T & H. S. Dattaraja) some amount of unobserved reversible shrinkage in the dry season may have been compensated by continuation of woody growth through the dry season.

Change in bias across the precipitation gradient and effect on growth – precipitation relationship

The slopes of the relationship between yearly Water Growth and yearly Dendrometer Growth (Figure 4) were highly and significantly positive for the dry forest plots, but not significantly different from zero for the moist forest plots. This indicates that along the precipitation gradient there is a progressive reduction in yearly bias in growth estimates due to hydrostatic bias.

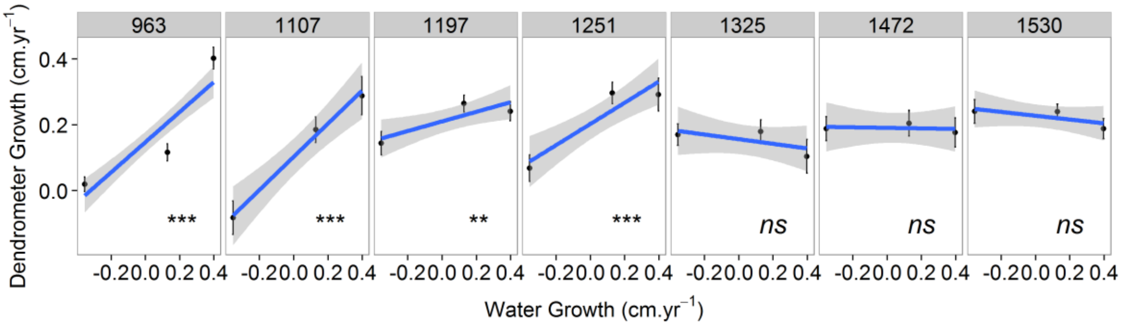


Figure 4: Water Growth in the three trees regressed against Dendrometer Growth of trees at each plot along the rainfall gradient. Panel headings are plot MAP values in mm. Plot mean growth rates with SE bars are shown. Gray envelopes are 95% confidence intervals for the linear regressions based on growth rates of all trees in the plot. Significance levels for the slopes are given ($\alpha = 0.05$); ^{ns} $P > 0.05$, $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.*

Before bias correction, slope values for Dendrometer Growth vs. MAP, linear relationships were significantly positive for the years 2011 and 2012, but significantly negative for the year 2013 (Figure 5a and 5b). After bias correction for the years 2011 and 2012, slope values were significantly positive, while for year 2013 they were not significantly different from zero. The slope of the 3-year mean growth vs. MAP linear relationship was not significantly different from zero before bias correction, but was marginally significantly different from zero after bias correction. This marginal difference arose because the correction caused a decrease of 4% to 12% in mean growth rates in the four dry forest plots, while wet plots did not require any correction (Figure 4).

Change in growth – diameter relationship and effect on growth – precipitation analysis

Across individual plots growth – DBH relationship appeared highly variable and no clear shift in trend was apparent (Figure 6). Broadly, in most dry forest plots, smaller size classes showed relatively higher growth rates leading to flat or even negative slopes, while moist forest plots showed consistently positive slopes. However, the limited number of trees in each size class for each plot – also reflected in large standard errors – did not allow us to systematically evaluate any shift in allometry based on analysis of individual plots.

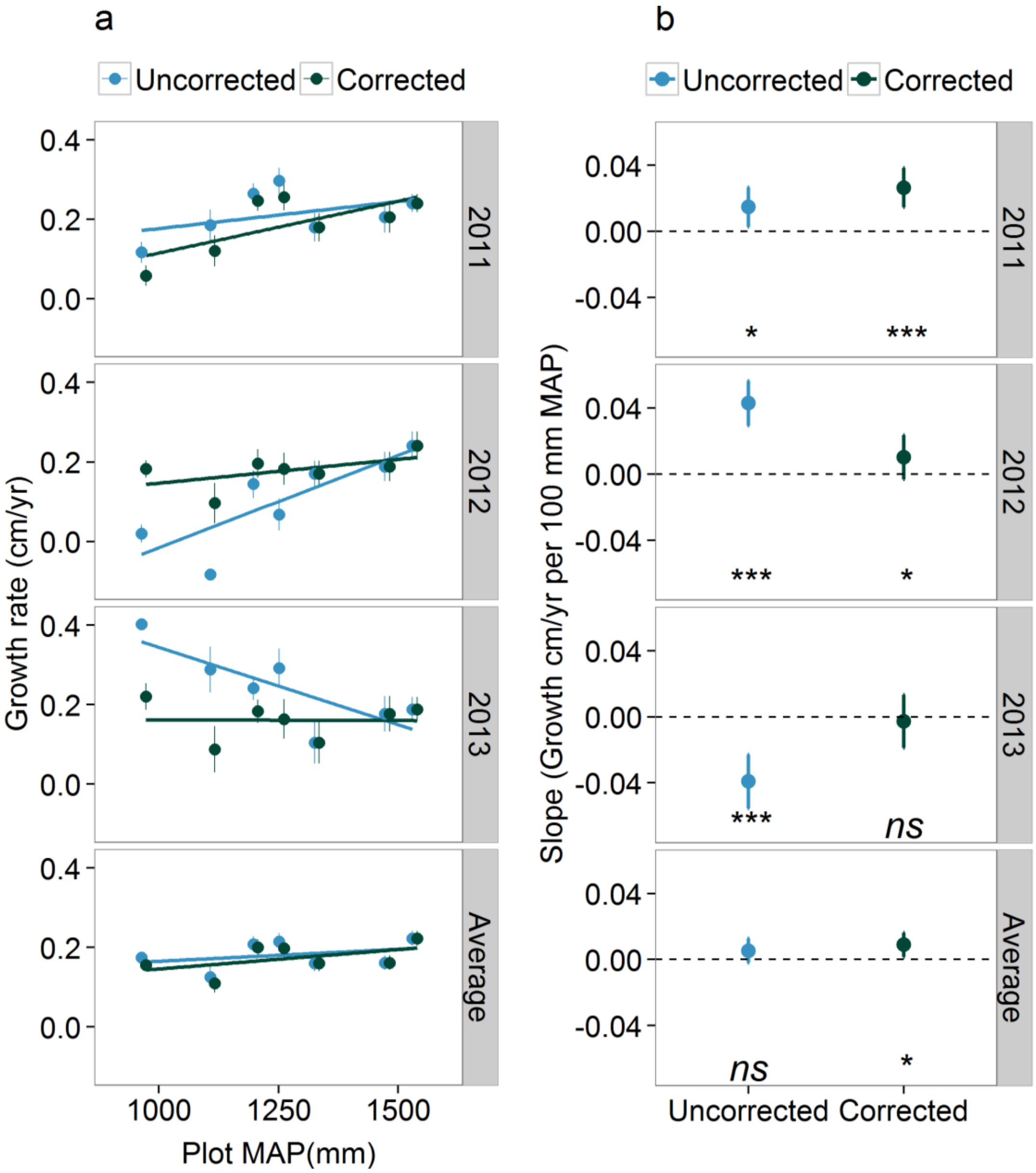


Figure 5: Linear regression fits of tree growth rates against MAP for year 2011, 2012 & 2013 and for 3-year average based on bias- uncorrected and bias-corrected growth rates (a). Plot mean growth rate with SE bars are shown. Corrected plot mean growth rates are shown slightly off the corresponding plot MAP for clarity. Effect sizes for slopes of the regressions with 95% confidence intervals are also shown (b). Significance levels for the slopes are given (H0 = slope is zero, α = 0.05); ^{ns} P > 0.05, P < 0.05; ** P < 0.01; *** P <0.001.*

Table 4: Coefficients for variables in Models M1 to M6 referred in the text with, goodness-of-fit statistics, AICs and p-values for model comparison are given. Coefficients are given for variables in their centered and scaled form. Numbers in squared brackets represent 95% confidence intervals. See in supplementary material Figure S1 for residuals vs. MAP and Figure S2 for residuals vs. DBH for Model M6.

Model	β_0 (Intercept)	β_1 (MAP)	β_2 (DBH)	β_3 (MAP:DBH)	τ (species SD)	σ (Resid. SD)	R^2 Marginal	R^2 Conditional	p-value for F test (H_0: All slopes = 0)	AIC	p-value for F (LMs) or Chi-sq (LMMs) tests
M1	0.184 [0.169, 0.198]	0.010 [-0.004, 0.025]					0.002	-	<0.01	-178.4	
M2	0.184 [0.169, 0.198]	0.006 [-0.009, 0.021]	0.027 [0.012, 0.041]				0.017	-	<0.001	-188.8	<0.001 (M1 and M2)
M3	0.185 [0.169, 0.198]	-0.021 [-0.046, 0.003]	-0.127 [-0.238, -0.016]	0.161 [0.046, 0.277]			0.025	-	<0.001	-194.3	<0.01 (M2 and M3)
M4	0.185 [0.155, 0.214]	0.000 [-0.019, 0.019]			0.088	0.195	0.000	0.168		-220.0	
M5	0.188 [0.158, 0.218]	-0.011 [-0.031, 0.010]	0.037 [0.019, 0.055]		0.090	0.192	0.027	0.205		-234.2	<0.001 (M4 and M5)
M6	0.189 [0.158, 0.219]	-0.040 [-0.070, -0.009]	-0.115 [-0.232, 0.003]	0.159 [0.037, 0.281]	0.097	0.201	0.034	0.216		-238.7	<0.05 (M5 and M6)

When evaluating the three linear models (M1, M2, M3; Table 4), the term MAP did not show significant effect on growth alone (M1), or in an additive (M2) or interactive effect with DBH (M3). However, growth positively, but marginally, increased with DBH in the case of additive model (M2); while with model M3 growth significantly decreased with DBH, but significantly increased with the MAPxDBH interaction term. This indicates a shift in growth – DBH allometric relationship along the gradient. However, the three models had poor goodness-of-fits, with M3 having the best fit.

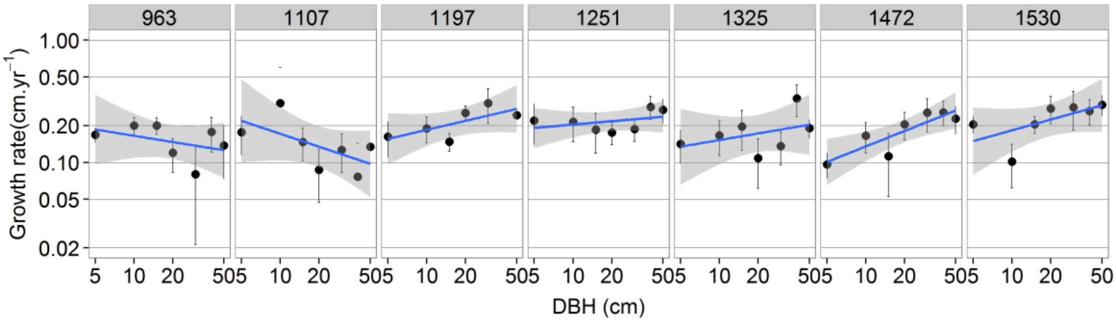


Figure 6: Observed growth – DBH relationship by plot MAP. Panel headings are plot MAP values in mm. Observed growth rates are 3-year mean growth rates. Tree DBH are grouped into classes of [5,10), [10,15), [15, 20), [20,30), [30,40), [40,50) and (50,80]. Mean growth rate and standard error for each size class is shown. Regression fits are shown with 95% confidence intervals in gray based on growth rates of all trees within a plot. Note the log-log scale.

Effect of species identity on precipitation gradient analysis

The linear mixed effect models (M4, M5 and M6) with the random species effect for the intercept had much higher and substantial goodness-of-fit (Table 4) compared to linear models M1, M2 and M3. Model M6 with the interaction term MAPxDBH had the highest goodness-of-fit and lowest AIC. Large variation in growth rates was found to be due to species identity.

A comparison between observed and predicted growth for model M3 and model M6 showed that species effect captured the observed hump-shape of the Growth-DBH curve for small trees in the dry forest (Figure 7). Across the gradient, compared to model M3, model M6 improved the goodness-of-fit statistic for the small trees (Figure 8) by a factor of 23 (R^2 = 0.007 and R^2 = 0.164 for M3 and M6, respectively), while only by a factor of 7 for large trees (R^2 = 0.035 and R^2 = 0.238, for M3 and M6, respectively).

Growth-DBH curve for the dry forest 50ha MFDP also showed a clear hump-shape structure across censuses (Figure 9), with growth rates increasing from ~1-5 cm DBH, then decreasing from ~5-15cm DBH and again showing an increasing trend ~20 cm DBH onwards.

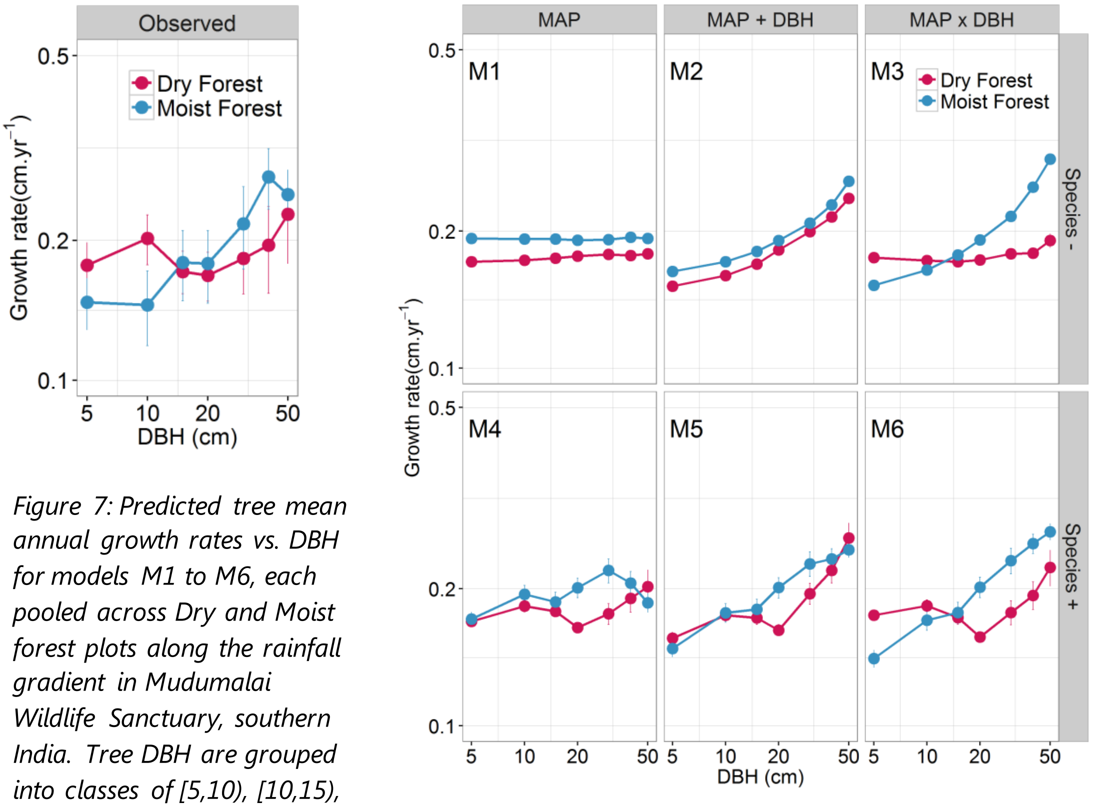


Figure 7: Predicted tree mean annual growth rates vs. DBH for models M1 to M6, each pooled across Dry and Moist forest plots along the rainfall gradient in Mudumalai Wildlife Sanctuary, southern India. Tree DBH are grouped into classes of [5,10), [10,15), [15, 20), [20,30), [30,40), [40,50) and [50,80] cm DBH. Mean growth rate and standard error for each size class is shown.

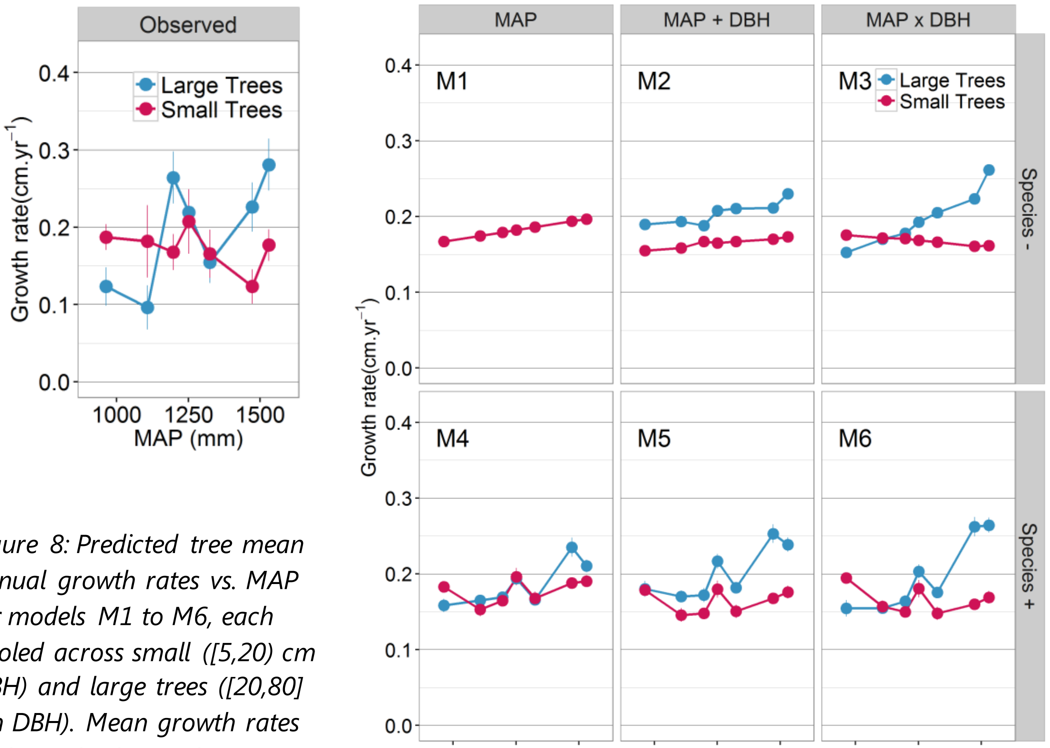


Figure 8: Predicted tree mean annual growth rates vs. MAP for models M1 to M6, each pooled across small ([5,20) cm DBH) and large trees ([20,80] cm DBH). Mean growth rates and standard error bars are shown for each plot

Discussion

This study showed significant shift in measurement bias and growth – diameter allometry of trees along a precipitation gradient in a seasonally dry tropical forest. Species composition also contributed to the shift in growth – diameter allometry.

Correction of bias due to water-induced fluctuations, using the novel method proposed by Chitra–Tarak et al. (2015), dramatically affected plot mean growth – MAP gradient relationship annually, but only marginally for plot mean growth rates across the three years of this study. The low bias found in mean growth across the three years of this study suggests that the tree water-status at the beginning and end of the three years was similar. This does not imply that mean growth rates across several years are always free from bias but would depend on the difference in tree water-status at the ends of the interval.

These results suggest that the method, initially aimed to improve estimation of plot mean growth – water availability relationship based on temporal studies that use PSP censuses of multi-annual intervals (Chitra-Tarak et al., 2015), can also be applied across a spatial precipitation gradient, at a much finer temporal scale and for growth studies using dendrometer bands. To our knowledge, this is the first report demonstrating a shift in the amplitude of bias due to water-induced fluctuations along a precipitation gradient, and its possible strong influence on the growth – gradient analysis.

Before bias correction, growth – MAP relationship showed a highly positive trend in the year 2012, followed by a highly negative trend for the year 2013 (Figure 5). Perhaps the positive trend in the year 2012 could be attributed to drought, causing relatively lower growth in drier compared to moister forest. However, to explain the negative trend of year 2013 with normal precipitation would require an unlikely explanation e.g., dry forest trees showing extremely high growth rates due to release from drought stress. Alternatively, the highly positive growth trend in 2012 and highly negative trend in 2013 could be explained if trees in dry forest plots, but not moist forest plots, were in a shrunk state due to low water-status at the time of measurement (see Table 2) in the dry season following the drought year of 2012 (Mar 2013) as compared to the water-status in the preceding and succeeding years (dry season of 2012 and 2014, respectively). The yearly bias due to water induced fluctuations, and its shift along the gradient, shown in this study, explain this pattern of opposite yearly trends in a much simpler way, and shows that bias correction led to a more consistent growth trend across years.

This meant that before correction, band dendrometer measurements were underestimating growth during the drought year 2012 in the dry forest, while overestimating it for the following year. The finding that the drought year had not resulted in a strong reduction of woody growth as compared to normal years is consistent with long-term hydrological modeling in the same region (Ruiz et al., 2010), which suggests that during this period the deep weathered saprolite (weathered rock) reservoir was at one of its highest levels of replenishment. It is then likely that during the drought of 2012, trees in the dry forest were able to maintain reasonable level of growth by taking up water available in the deep saprolite layers.

In this study the extent of slope of the linear relationship between proxy – Water Growth – in the three trees and Dendrometer Growth of individual trees at a given plot was taken as the extent of yearly bias at the given plot. For the moist forest plots the slope was not significantly different from zero, suggesting that yearly bias was absent. It is possible that the yearly bias measured in the three trees from a drier part of the gradient did not fully capture the bias in wetter parts, possibly underestimating it, and thus overestimating the impact of bias correction on growth – precipitation relationship. This could be verified and the approach improved by measuring the Ring Growth from trees within each plot and/or for various size classes, and using it to correct bias in the tree community of the respective plots and size classes.

This study found a marked shift in growth – DBH relationship along the gradient as evidenced in the significant interaction between MAP and DBH in both linear models, M3 and M6 (Table 4). Although variations in size-dependency in growth were observed by Condit et al. (2004) at three sites on a precipitation gradient, to our knowledge, this is the first time such a shift is demonstrated through a model. The effect of individual or combined explanatory variables can be visualized both by comparing growth – DBH relationships plotted for dry and moist forest plots, and growth – MAP relationships for small and large size classes for each of the models (Figures 7, 8). In this representation, model M1 & M4 act as controls for any effect of DBH. The observed variation seen in growth for M1 & M4 against DBH is then due to other reasons captured in these models: either rainfall (M1), or rainfall and species turnover (M4). Note that the minor variation visible for M1 in Figure 7 with DBH is due to MAP variation within dry and moist forest plots that the trees in the given size classes belong to.

For simple linear models (M1 to M3), adding the interaction term in model M3 brings out the shift in growth-DBH allometry along the precipitation gradient in two ways (a) a differential effect of MAP with tree size for dry and moist plots (Figure 7) and (b) a positive growth trend with MAP for large trees and a negative growth trend for small trees (Figure 8), otherwise not accounted by M1 or M2.

For mixed effects models (M4 to M6), Figures 7 and 8 illustrate that merely adding the species random effect for intercept to the effect of MAP (M4), accounted for the distinct pattern of growth – DBH curves for small trees in dry forest plots (Figure 7) and a part of the variability in the observed growths rates across different plots (Figure 8). This variability due to species was preserved when DBH (M5) and MAPxDBH interaction effects were added (M6). The species effect could have been due to presence of certain species in only certain size classes with the additional effect of turnover of species across forest plots. However, limited sample sizes constrain us from further evaluating this. Future research using larger dataset from the present site should also investigate the relative contribution of shift in allometry due to within species response versus that due to species turnover.

The faster growth rates of smaller stems in the dry compared to moist forest could arise due to greater light availability and reduced competition (Muller-Landau et al., 2006). This could also arise from greater occurrence of species adapted to these fire-prone dry forests, as growth rates of juvenile trees in savanna systems are known to be higher as an adaptation to escape from fire trap (Bond, 2008; Bond et al., 2012). Indeed the dry forests in this study experience frequent ground fires, and juveniles in burnt areas are found to have faster growth rates than in un-burnt areas (Mondal and Sukumar, 2015).

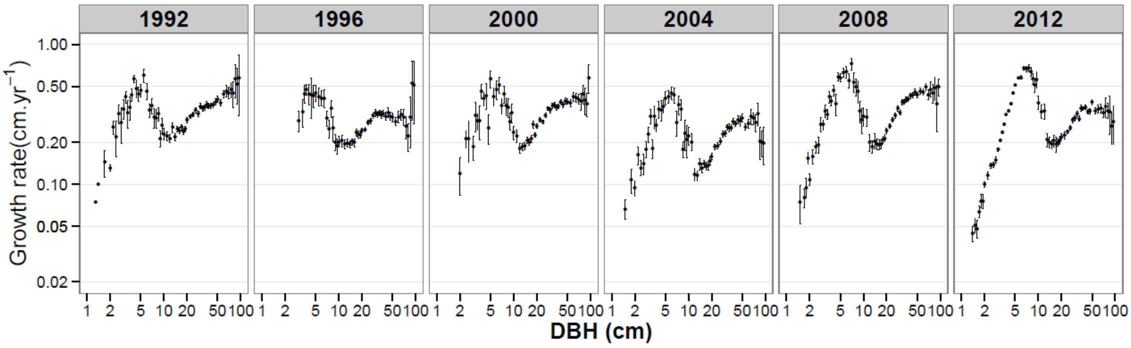


Figure 9: Observed growth – DBH relationship at the 50ha MFDP for each 4-year scale census interval from 1988-2012, such that panel 1992 repreesnts growth from 1988-1992. Error bars represent 95% bootstrapped confidence interval for a given size class. Note the log-log scale.

Interestingly, the size-specific trends in growth-rates at the dry forest 50 ha MFDP (Figure 9) strikingly match against the differential size-specific causes of mortality in this forest. Fire is the primary cause of mortality for the class 1-5cm DBH, which showed high growth rates, while mortality due to large-mammals such as elephants is the primary cause of mortality for the following size class 5-10 cm DBH, which showed decreasing trend in growth rates (Sukumar et al., 2005; Suresh et al., 2011). It could be hypothesized that herbivory or injury due to large-mammals may also play a role in the reducing trend of growth rates for this size class. The relative roles of light, fire and herbivory in shaping the distinct allometric patterns along this precipitation gradient should make an interesting topic for a study.

We also investigated if faster growth rates found in the smaller size class is due to disproportionate contribution from species whose maximum sizes are small and have inherently faster growth rates. We found that species with small (for example, HELI, CASF) and large maximum sizes (for example, LAGL and GRET) can both have inherent fast growth rates and even when small. Although two small sized species (HELI and CASF) did contribute disproportionately to the fast growth rates in size class 1-7 cm DBH, both small (CASF) and large (LAGL) maximum size tree species disproportionately contributed to the fast growth rates in the size class 7-10 (Figure 10).

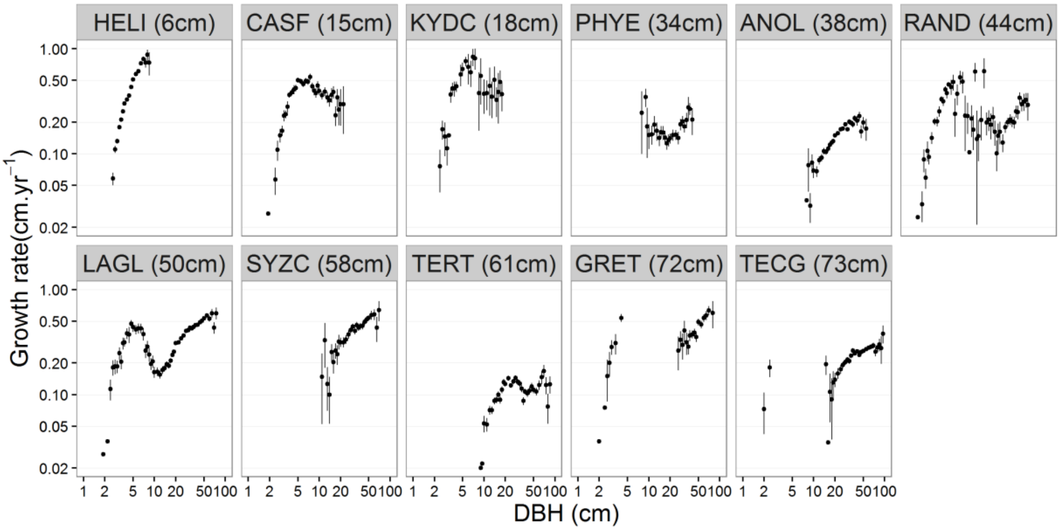


Figure 10. Observed growth – DBH relationship at the 50ha MFDP by species, mean growth rate across all 4-yr scale intervals from 1988-2012 is used for a tree. Each panel represents a species with maximum size based on 95 percentile for the given size calss given in brackets. Error bars represent 95%bootstrapped confidence interval. Note the log-log scale. See page for species codes. HELI and KYDC represent Helicteres isora (L.) and Kydia calycina, respectively. See page 145 for other species codes.

The observed effect of shift in growth – DBH relationships on the gradient analysis is highly relevant in the context of 'space for time' substitution modeling. Although valid for analyzing average growth rate variation along climate gradients, models not including DBH (Toledo et al., 2011), or including DBH only as an additive effect (Rapp et al., 2012), would lead to inaccurate assessments if they were to be used for analyzing impact of climate change on carbon sequestration or forest dynamics. We claim that using models with MAPxDBH interaction is likely to improve temporal projections inferred from spatial analysis. In our case it revealed that growth rates of large trees are more sensitive to precipitation gradient, which is noteworthy given that most of the forest biomass and carbon is present and accumulated in large trees (Stephenson et al., 2014). For forest dynamics modeling, the fact that the faster growth of small trees in dry vs. moist forest that the model captured was due mostly to species identities of trees might constrain the use of 'space for time' substitution modeling in this case. This is particularly relevant for understanding and predicting savanna – forest biome shifts since modeling ecosystem response to increasing fire and drying conditions under climate change is urgently required, but poorly understood (IPCC, 2014).

Future research should also investigate sensitivity of large vs. small trees to variability in water availability, besides the sensitivity to change in total annual precipitation along the gradient. Finally, in case of increased frequency and intensity of droughts as expected under climate change scenarios, we expect that frequency and intensity of bias in growth estimates would also increase due to greater likely differences in water-status of the trees from one census to another. This is especially likely in seasonal environments either in the tropics or temperate regions. We suggest that these factors must be carefully evaluated and appropriately accounted for in studies of tree growth – climate relationships.

Acknowledgements

This study was financially supported by Ministry of Environment and Forest, Govt. of India. We thank Tamil Nadu Forest Department for research permissions to work at Mudumalai. This work would not have been possible without the hard work of numerous tribal and local personnel in Mudumalai Wildilife Sanctuary, and CES staff over the past three decades. We thank Hemant Borgaonkar and Naveen Gandhi of IITM, Pune for helping with tree-ring width measurements. RCT was supported by CSIR Junior and Senior Research Fellowships. RS was a J. C. Bose National Fellow during the period of this study.

References

Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A.M., Alonso, A., Baltzer, J.L., Basset, Y., Bourg, N.A., Broadbent, E.N., Brockelman, W.Y., Bunyavejchewin, S., Burslem, D.F.R.P., Butt, N., Cao, M., Cardenas, D., Chuyong, G.B., Clay, K., Cordell, S., Dattaraja, H.S., Deng, X., Detto, M., Du, X., Duque, A., Erikson, D.L., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Foster, R.B., Giardina, C.P., Gilbert, G.S., Gunatilleke, N., Gunatilleke, S., Hao, Z., Hargrove, W.W., Hart, T.B., Hau, B.C.H., He, F., Hoffman, F.M., Howe, R.W., Hubbell, S.P., Inman-Narahari, F.M., Jansen, P.A., Jiang, M., Johnson, D.J., Kanzaki, M., Kassim, A.R., Kenfack, D., Kibet, S., Kinnaird, M.F., Korte, L., Kral, K., Kumar, J., Larson, A.J., Li, Y., Li, X., Liu, S., Lum, S.K.Y., Lutz, J.A., Ma, K., Maddalena, D.M., Makana, J.-R., Malhi, Y., Marthews, T., Mat Serudin, R., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Mizuno, T., Morecroft, M., Myers, J.A., Novotny, V., de Oliveira, A.A., Ong, P.S., Orwig, D.A., Ostertag, R., den Ouden, J., Parker, G.G., Phillips, R.P., Sack, L., Sainge, M.N., Sang, W., Sri-ngernyuang, K., Sukumar, R., Sun, I.-F., Sungpalee, W., Suresh, H.S., Tan, S., Thomas, S.C., Thomas, D.W., Thompson, J., Turner, B.L., Uriarte, M., Valencia, R., Vallejo, M.I., Vicentini, A., Vrška, T., Wang, X., Wang, X., Weiblen, G., Wolf, A., Xu, H., Yap, S., Zimmerman, J., 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Glob. Change Biol. 21, 528–549. doi:10.1111/gcb.12712

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., Vargas, P.N., Pitman, N.C.A., Silva, J.N.M., Martínez, R.V., 2004. Increasing biomass in Amazonian forest plots. Philos. Trans. R. Soc. B Biol. Sci. 359, 353–365.

Baltzer, J.L., Davies, S.J., Bunyavejchewin, S., Noor, N.S.M., 2008. The role of desiccation tolerance in determining tree species distributions along the Malay–Thai Peninsula. Funct. Ecol. 22, 221–231. doi:10.1111/j.1365-2435.2007.01374.x

Becknell, J.M., Kissing Kucek, L., Powers, J.S., 2012. Aboveground biomass in mature and secondary seasonally dry tropical forests: A literature review and global synthesis. For. Ecol. Manag. 276, 88–95. doi:10.1016/j.foreco.2012.03.033

Berthelot, M., Friedlingstein, P., Ciais, P., Dufresne, J.-L., Monfray, P., 2005. How uncertainties in future climate change predictions translate into future terrestrial carbon fluxes. Glob. Change Biol. 11, 959–970. doi:10.1111/j.1365-2486.2005.00957.x

Bonan, G.B., 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science 320, 1444–1449. doi:10.1126/science.1155121

Bond, W.J., 2008. What Limits Trees in C4 Grasslands and Savannas? Annu. Rev. Ecol. Evol. Syst. 39, 641–659. doi:10.1146/annurev.ecolsys.39.110707.173411

Bond, W.J., Cook, G.D., Williams, R.J., 2012. Which trees dominate in savannas? The escape hypothesis and eucalypts in northern Australia. Austral Ecol. 37, 678–685. doi:10.1111/j.1442-9993.2011.02343.x

Bongers, F., Poorter, L., Hawthorne, W.D., 2004. The forests of Upper Guinea: Gradients in large species composition., in: Poorter, L., Bongers, F., Kouame, F.N., Hawthorne, W.D. (Eds.), Biodiversity of West African Forests. An Ecological Atlas of Woody Plant Species. CABI Publishing, Oxford, UK, pp. 41–52.

Chitra-Tarak, R., Ruiz, L., Pulla, S., Dattaraja, H.S., Suresh, H.S., Sukumar, R., 2015. And yet it shrinks: A novel method for correcting bias in forest tree growth estimates caused by water-induced fluctuations. For. Ecol. Manag. 336, 129–136. doi:10.1016/j.foreco.2014.10.007

Clark, D.A., Clark, D.B., 2011. Assessing Tropical Forests' Climatic Sensitivities with Long-term Data. Biotropica 43, 31–40. doi:10.1111/j.1744-7429.2010.00654.x

Clark, D.B., Clark, D.A., Oberbauer, S.F., 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO^2. Glob. Change Biol. 16, 747–759. doi:10.1111/j.1365-2486.2009.02004.x

Clark, J.S., Wolosin, M., Dietze, M., Ibanez, I., LaDeau, S., Welsh, M., Kloeppel, B., 2007. Tree growth inference and prediction from diameter censuses and ring widths. Ecol. Appl. 17, 1942–1953. doi:10.1890/06-1039.1

Comita, L.S., Engelbrecht, B.M.J., 2014. Drought as a driver of tropical tree species regeneration dynamics and distribution patterns, in: Coomes, D.A., Burslem, D.F.R.P., Simonson, W.D. (Eds.), Forests and Global Change, Ecological Reviews. Cambridge University Press.

Condit, R., 1998. Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots. Springer-Verlag, Berlin.

Condit, R., Aguilar, S., 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. doi:10.1017/S0266467403001081

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187. doi:10.1038/35041539

Cushman, K.C., Muller-Landau, H.C., Condit, R.S., Hubbell, S.P., 2014. Improving estimates of biomass change in buttressed trees using tree taper models. Methods Ecol. Evol. 5, 573–582. doi:10.1111/2041-210X.12187

Dattaraja, H.S., Mondal, N., Pulla, S., Suresh, H.S., Bhamnaiah, C.M., Sukumar, R., 2013. Spatial interpolation of rainfall for Mudumalai Wildlife Sanctuary and Tiger Reserve, Tamil Nadu, India. (CES Technical Report). Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India.

Davidar, P., Puyravaud, J.P., Leigh, E.G., 2005. Changes in rain forest tree diversity, dominance and rarity across a seasonality gradient in the Western Ghats, India. J. Biogeogr. 32, 493–501. doi:10.1111/j.1365-2699.2005.01165.x

Davidar, P., Rajagopal, B., Mohandass, D., Puyravaud, J.-P., Condit, R., Wright, S.J., Leigh, E.G., 2007. The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. Glob. Ecol. Biogeogr. 16, 510–518. doi:10.1111/j.1466-8238.2007.00307.x

Dirzo, R., Raven, P.H., 2003. Global State of Biodiversity and Loss. Annu. Rev. Environ. Resour. 28, 137–167. doi:10.1146/annurev.energy.28.050302.105532

Dunne, J.A., Saleska, S.R., Fischer, M.L., Harte, J., 2004. Integrating experimental and gradient methods in ecological climate change research. Ecology 85, 904–916. doi:10.1890/03-8003

Engelbrecht, B., Comita, L., Condit, R., Kursar, T., Tyree, M., Turner, B., Hubbell, S., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. NATURE 447, 80–U2. doi:10.1038/nature05747

Feeley, K.J., Joseph Wright, S., Nur Supardi, M.N., Kassim, A.R., Davies, S.J., 2007. Decelerating growth in tropical forest trees. Ecol. Lett. 10, 461–469. doi:10.1111/j.1461-0248.2007.01033.x

Gentry, A.H., 1988. Changes in Plant Community Diversity and Floristic Composition on Environmental and Geographical Gradients. Ann. Mo. Bot. Gard. 75, 1–34. doi:10.2307/2399464

Goswami, B.N., Venugopal, V., Sengupta, D., Madhusoodanan, M.S., Xavier, P.K., 2006. Increasing Trend of Extreme Rain Events Over India in a Warming Environment. Science 314, 1442–1445. doi:10.1126/science.1132027

Grace, J., José, J.S., Meir, P., Miranda, H.S., Montes, R.A., 2006. Productivity and carbon fluxes of tropical savannas. J. Biogeogr. 33, 387–400. doi:10.1111/j.1365-2699.2005.01448.x

Hall, J.B., Swaine, M.D., 1976. Classification and Ecology of Closed-Canopy Forest in Ghana. J. Ecol. 64, 913–951. doi:10.2307/2258816

Hassan, R.M., Scholes, R., Ash, N. (Eds.), 2005. Ecosystems and Human Well-Being: Current State and Trends. Island Press, Washington, DC.

Hoffmann, W.A., Schroeder, W., Jackson, R.B., 2003. Regional feedbacks among fire, climate, and tropical deforestation. J. Geophys. Res. Atmospheres 108, 4721. doi:10.1029/2003JD003494

Hulme, M., Viner, D., 1998. A Climate Change Scenario for the Tropics. Clim. Change 39, 145–176. doi:10.1023/A:1005376007729

IPCC, 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., K, M.-N.D., 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., 2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006. doi:10.1038/nature07771

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., Nobre, C.A., 2008. Climate Change, Deforestation, and the Fate of the Amazon. Science 319, 169–172. doi:10.1126/science.1146961

Malhi, Y., Wright, J., 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 359, 311–329. doi:10.1098/rstb.2003.1433

Matthews, H.D., Eby, M., Ewen, T., Friedlingstein, P., Hawkins, B.J., 2007. What determines the magnitude of carbon cycle-climate feedbacks? Glob. Biogeochem. Cycles 21, GB2012. doi:10.1029/2006GB002733

Mondal, N., Sukumar, R., 2015. Regeneration of juvenile woody plants after fire in a seasonally dry tropical forest of Southern India. Biotropica 47, 330–338.

Muller-Landau, H.C., Condit, R.S., Chave, J., Thomas, S.C., Bohlman, S.A., Bunyavejchewin, S., Davies, S., Foster, R., Gunatilleke, S., Gunatilleke, N., Harms, K.E., Hart, T., Hubbell, S.P., Itoh, A., Kassim, A.R., LaFrankie, J.V., Lee, H.S., Losos, E., Makana, J.-R., Ohkubo, T., Sukumar, R., Sun, I.-F., Nur Supardi, M.N., Tan, S., Thompson, J., Valencia, R., Muñoz, G.V., Wills, C., Yamakura, T., Chuyong, G., Dattaraja, H.S., Esufali, S., Hall, P., Hernandez, C., Kenfack, D., Kiratiprayoon, S., Suresh, H.S., Thomas, D., Vallejo, M.I., Ashton, P., 2006. Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. Ecol. Lett. 9, 575–588. doi:10.1111/j.1461-0248.2006.00904.x

Murphy, P.G., Lugo, A.E., 1986. Ecology of Tropical Dry Forest. Annu. Rev. Ecol. Syst. 17, 67–88.

Neelin, J.D., Münnich, M., Su, H., Meyerson, J.E., Holloway, C.E., 2006. Tropical drying trends in global warming models and observations. Proc. Natl. Acad. Sci. 103, 6110–6115. doi:10.1073/pnas.0601798103

Phillips, Malhi, Higuchi, Laurance, Nunez, Vasquez, Laurance, Ferreira, Stern, Brown, Grace, 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science 282, 439–442.

Poorter, L., Bongers, F., Kouame, F.N., Hawthorne, W.D., 2004. Biodiversity of West African Forests: An Ecological Atlas of Woody Plant Species. CABI Publishing, Oxford, UK.

Priya, P.B., Bhat, K.M., 1998. False ring formation in teak (Tectona grandis L.f.) and the influence of environmental factors. For. Ecol. Manag. 108, 215 – 222. doi:DOI: 10.1016/S0378-1127(98)00227-8

Pumijumnong, N., 2013. Dendrochronology in Southeast Asia. Trees-Struct. Funct. 27, 343–358. doi:10.1007/s00468-012-0775-7

Rao, K.S., Dave, Y.S., 1981. Seasonal variations in the cambial anatomy of Tectona grandis (Verbenaceae). Nord. J. Bot. 1, 535–542. doi:10.1111/j.1756-1051.1981.tb00719.x

Rapp, J.M., Silman, M.R., Clark, J.S., Girardin, C.A.J., Galiano, D., Tito, R., 2012. Intra- and inter-specific tree growth across a long altitudinal gradient in the Peruvian Andes. Ecology. doi:10.1890/11-1725.1

Ratnam, J., Bond, W.J., Fensham, R.J., Hoffmann, W.A., Archibald, S., Lehmann, C.E.R., Anderson, M.T., Higgins, S.I., Sankaran, M., 2011. When is a "forest" a savanna, and why does it matter? Glob. Ecol. Biogeogr. 20, 653–660. doi:10.1111/j.1466-8238.2010.00634.x

R Core Team, 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Australia.

Roxy, M.K., Ritika, K., Terray, P., Murtugudde, R., Ashok, K., Goswami, B.N., 2015. Drying of Indian subcontinent by rapid Indian Ocean warming and a weakening land-sea thermal gradient. Nat. Commun. 6, 7423. doi:10.1038/ncomms8423

Ruiz, L., Varma, M.R.R., Kumar, M.S.M., Sekhar, M., Maréchal, J.-C., Descloitres, M., Riotte, J., Kumar, S., Kumar, C., Braun, J.-J., 2010. Water balance modelling in a tropical watershed under deciduous forest (Mule Hole, India): Regolith matric storage buffers the groundwater recharge process. J. Hydrol. 380, 460–472. doi:10.1016/j.jhydrol.2009.11.020

Schuur, E.A.G., 2003. Productivity and Global Climate Revisited: The Sensitivity of Tropical Forest Growth to Precipitation. Ecology 84, 1165–1170. doi:10.1890/0012-9658(2003)084[1165:PAGCRT]2.0.CO;2

Sharma, B.D., Shetty, B.V., Vivekananthan, K., Rathakrishnan, N.C., 1977. Flora of Mudumalai Wildlife Sanctuary, Tamil Nadu. J. Bombay Nat. Hist. Soc. 75, 13–42.

Sheil, D., 2003. Growth assessment in tropical trees: large daily diameter fluctuations and their concealment by dendrometer bands. Can. J. For. Res. 33, 2027–2035. doi:10.1139/x03-121

Sheil, D., 1995. A critique of permanent plot methods and analysis with examples from Budongo Forest, Uganda. For. Ecol. Manag. 77, 11 – 34. doi:10.1016/0378-1127(95)03583-V

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507, 90–93. doi:10.1038/nature12914

Sukumar, R., Dattaraja, H.S., Suresh, H.S., Radhakrishnan, J., Vasudeva, R., Nirmala, S., Joshi, N.V., 1992. Long term monitering of vegetation in a tropical deciduous forest in Mudumalai, southern India. Curr. Sci. 62, 608–616.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Joshi, N.V., 1998. Dynamics of a tropical deciduous forest: population changes (1988 through 1993) in a 50-ha plot at Mudumalai, southern India.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Srinidhi, S., Nath, C., 2005. The dynamics of a tropical dry forest in India: climate, fire, elephants and the evolution of life-history strategies, in: Biotic Interactions in the Tropics, Ecological Reviews. Cambridge University Press.

Suresh, H.S., Dattaraja, H.S., Mondal, N., Sukumar, R., 2011. Seasonally Dry Tropical Forests in Southern India: An Analysis of Floristic Composition, Structure, and Dynamics in Mudumalai Wildlife Sanctuary, in: McShea, W.J., Davies, S.J., Bhumakphan, N. (Eds.), The Ecology and Conservation of Seasonally Dry Forests in Asia. Smithsonian Institution Scholarly Press, Washington, D.C.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prévost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P., Vásquez, R., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443, 444–447. doi:10.1038/nature05134

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., Leaño, C., Licona, J.C., Poorter, L., 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. J. Ecol. 100, 253–263. doi:10.1111/j.1365-2745.2011.01890.x

Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., Bongers, F., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J. Ecol. 99, 254–264. doi:10.1111/j.1365-2745.2010.01741.x

van der Werf, G.R., Dempewolf, J., Trigg, S.N., Randerson, J.T., Kasibhatla, P.S., Giglio, L., Murdiyarso, D., Peters, W., Morton, D.C., Collatz, G.J., Dolman, A.J., DeFries, R.S., 2008. Climate regulation of fire emissions and deforestation in equatorial Asia. Proc. Natl. Acad. Sci. U. S. A. 105, 20350–20355. doi:10.1073/pnas.0803375105

Wright, S.J., 2005. Tropical forests in a changing environment. Trends Ecol. Evol. 20, 553 – 560. doi:DOI: 10.1016/j.tree.2005.07.009

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media.

Chapter 6

Multi-scale precipitation patterns drive belowground niche partitioning and drought effects in a seasonally dry tropical forest

---

This chapter is being revised for submission to *Nature Plants*.

Abstract

Droughts can shift the function and composition of forests worldwide, but the underlying mechanisms are poorly understood, mostly because drought experienced by each tree depend on the complex interactions between root systems and below-ground water availability. Here we address this knowledge gap by proposing an analytical framework linking rainfall, belowground water status, water uptake depth, and plant growth and mortality. We applied a dynamic hydrological model to 20-yr long records of tree demography in a seasonally dry tropical forest in the Western Ghats, India, and found that key demographic responses to drought are explained by the interplay between decoupled patterns of rainfall and water storage by depth that develop over multi-annual or even decadal time spans and the distinct rooting strategies we identified across fourteen common species. Although all species showed low and steady mortality through normal droughts, mortality dramatically increased with deep rootedness after an exceptionally dry period. Here, we expect a trade-off, with selection for shallow-rooted species in exceptional droughts, but more steady carbon gain from the deep-rooted species otherwise. This changes our understanding of how hydrological niches operate for trees. The novel analytical framework proposed here opens up an avenue to better understand tree species coexistence in diverse forest communities, and improve mechanistic predictions of forest productivity and compositional change under future drought.

Introduction

Improving predictions of future forest structure and function is essential to global estimates of atmospheric carbon, climate systems, and biodiversity. Drought-induced tree mortality is now thought to be a major threat to temperate and tropical forests (Allen *et al.* 2010, 2015) and much of the concern for forest response to climate centres around tree species response to drought (McDowell *et al.* 2008; Choat *et al.* 2012; Anderegg *et al.* 2013b). Dynamic Global Vegetation Models generally cannot predict drought-induced mortality accurately because many critical processes that lead from meteorological drought to death are unknown or poorly understood (McDowell *et al.* 2008; Anderegg, Anderegg & Berry 2013a; Meir, Mencuccini & Dewar 2015; Allen *et al.* 2015). Especially lacking are estimations of plant-available water vertically belowground on temporal scales at which droughts unfold. Water-uptake, which is mediated by hydraulic traits and root depth, further determines the drought actually experienced by trees, which can be different across species. Quantifying species-specific experienced drought remains a challenge, as multiple spatio-temporal niches by rooting depth may evolve from stochastic precipitation events, creating complex temporal patterns of water availability through the vadose zone (Schwinning 2010; Schwinning & Kelly 2013)—the unsaturated zone made up of soil and weathered rock above the ground water table. This pattern of diverse "experienced' droughts can lead to apparently idiosyncratic responses of observed tree growth to precipitation.

The current framework to understand drought-driven mortality focuses on above-ground strategies for water regulation (physiological or anatomical features such as hydraulic safety-margins (McDowell *et al.* 2008; Choat *et al.* 2012), vessel architecture, or stomatal regulation (McDowell *et al.* 2008)). From the above-ground perspective, species are positioned along the axis of isohydry (maintenance of high water potential through stomatal regulation at the cost of carbon assimilation, with the risk of carbon starvation under prolonged drought) and anisohydry (maintenance of high gas exchange at low plant water potential with greater vulnerability to hydraulic failure under intense drought due to narrow hydraulic safety margins) (McDowell *et al.* 2008; Skelton, West & Dawson 2015). The consequences of these strategies on plant growth and mortality, however, depend on realized and not hypothesized access to water sources, the former being an interaction between rooting systems, plant hydraulic traits and dynamics of water belowground. Unfortunately, most studies linking drought impacts to water availability, characterise the latter only by precipitation or surface soil moisture patterns, and ignore the complex, but critical, dynamics of belowground water at depth that trees depend upon (Rodriguez-Iturbe 2000). Few recent studies demonstrate the importance of Hydrological Niche Separation (HNS) to explain species co-existence based on belowground observations (Silvertown, Araya & Gowing 2015). However, due to experimental constrains, they are limited to few species (typically 2) and focus on niches operating at very shallow depth (about 1m).

We provide a new analytical framework to test demographic response to drought in natural biodiverse forests and to understand how HNS operates for trees. This framework is based on the hypothesis that the dynamics of water availability across depth is controlled by evapotranspiration across the whole forest community, whereas individual trees or species are constrained by water availability, but do not affect it. We estimated species-specific parameters governing water-uptake depth by inversion of a new model of tree water-stress (see Methods). The inversion was carried out on observations of tree growth from a seasonally dry tropical forest of the Western Ghats, India, in the long-monitored 50 ha Mudumalai Forest Dynamics Plot (Sukumar *et al.* 1992, 2005) (MFDP) and robust simulations of daily water availability in the soil, as well as in the shallow and deep weathered rock zones above the water table (i.e. the vadose zone, see Methods). These simulations were obtained from a dynamic hydrological model—COMFORT—previously developed, calibrated and validated in the nearby Mulehole observatory (Ruiz *et al.* 2010). Based on the estimated uptake parameters, we simulated species-specific dynamics of water-uptake by depth over two decades.

Results and Discussion

The hydrological model COMFORT acts as a low-pass filter that most parsimoniously allows accurate conversion of the observed high frequency variation in the rainfall pattern into the observed low frequency variation in groundwater levels by redistributing—in space and time—this signal dampening. In the study site, it revealed the decoupling between the temporal dynamics of rainfall and water at depth, with high frequency variations at shallower depths reflecting daily or seasonal rainfall, and low frequency variations at deeper depths reflecting memory of decadal patterns in rainfall (Fig. 1, Supplementary Fig. 2). Note that the exceptional succession of four drought years from 2000–2003 led to the drying of the deep vadose zone for more than two years with a lag, offering insights into how a range of drying down times exposes the importance of vertical locations of water-uptake.

The dynamic water-stress model introduced here is based on the assumption that deviation from growth potential is a function of water-stress index—water supply-to-demand ratio (see Methods). The inversion of this water-stress model allows us to estimate uptake parameters that best explain the observed temporal variations in tree growth given the variations in water availability by depth. We carried out the inversion

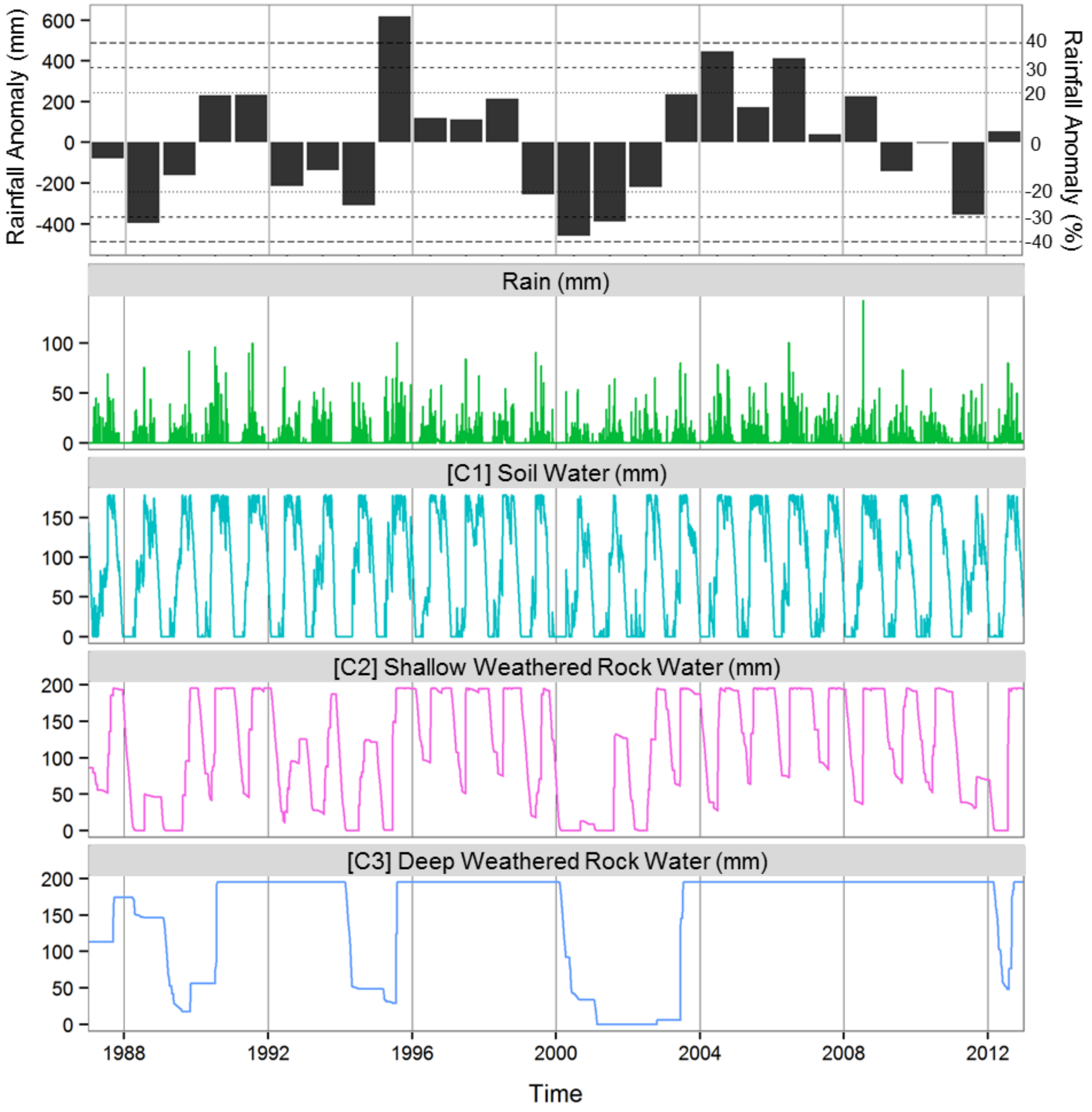


Figure 1 | Belowground water availability as estimated by the hydrological model COMFORT at MFDP, Mudumalai National Park, southern India. 1988 to 2013 time series—from top to bottom—of annual rainfall anomaly, observed daily rainfall, simulated water content of three belowground compartments. *Grey vertical lines mark Mudumalai growth census year-ends. The bottom of each compartment is estimated to be 2 m, 14 m and 26 m from the surface, respectively. For 1988-2012, correlations (Pearson's product-moment correlation coefficient, r) between mean annual compartment water content for C1, C2 and C3 and annual rainfall (n = 25) were 0.82, 0.76 and 0.34, with P <0.001, <0.001 and 0.16, respectively; and those for monthly rainfall (n = 300) were 0.58, 0.02 and 0.03 with P <0.001, 0.7 and 0.6, respectively.*

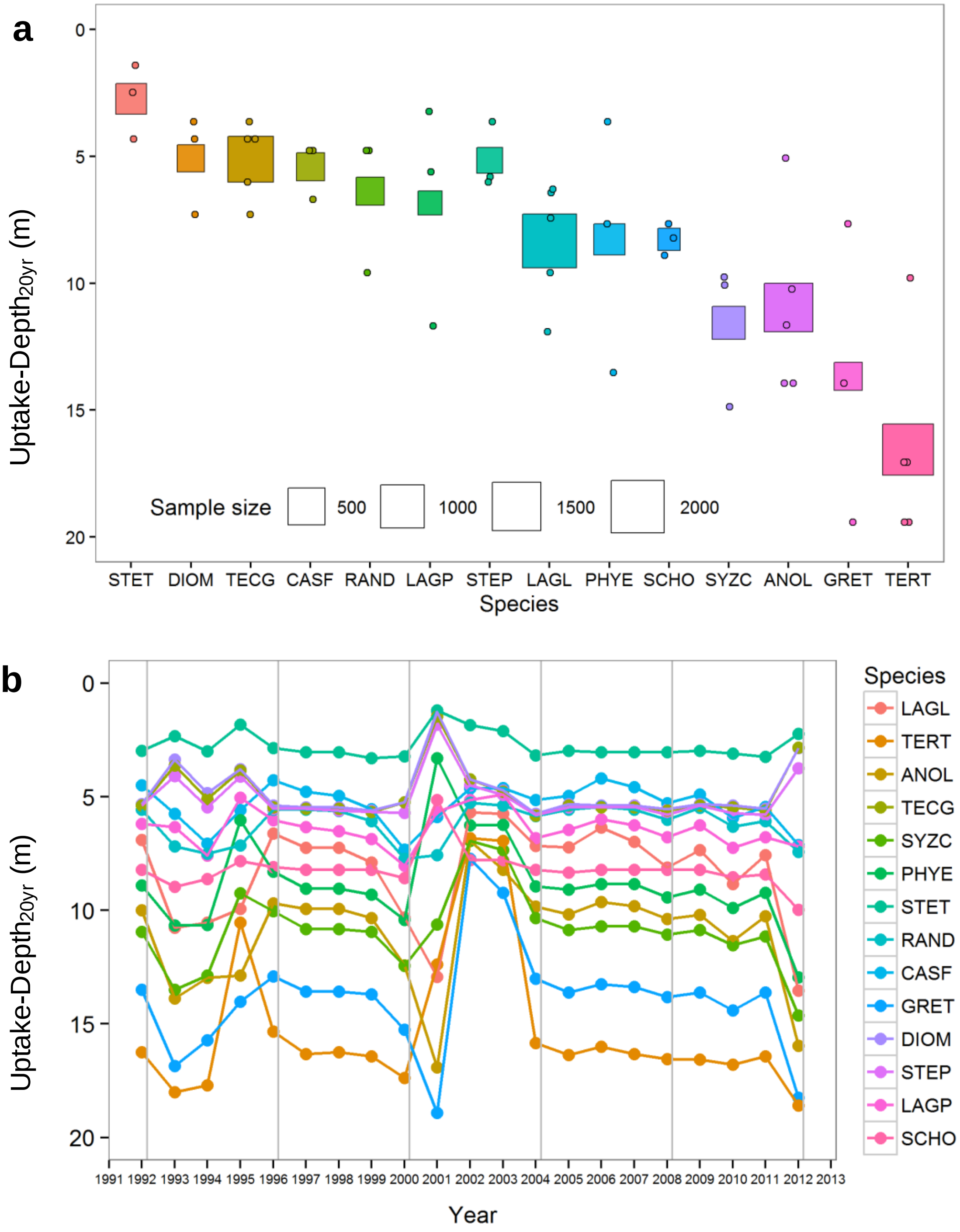


Figure 2 | Estimated water-uptake depth variation across species at MFDP. a *Uptake-Depth$_{20yr}$ for each quantile based size class within species (circles), ordered by species median Uptake-Depth$_{20yr}$ (n =5 or 3 size classes depending on species). Each size class represents 13 to 441 trees depending on species (see Supplementary Table 2). Circles are slightly jittered horizontally for clarity. Species Uptake-Depth$_{20yr}$ (mean across size classes, n =5 or 3) is shown in squares, with symbol size proportional to the total sample size of trees for a given species. Colors vary by species.* ***b*** *Time series of species Uptake-Depth$_{annual}$ (mean across size classes, n =5 or 3) from 1992-2012. See Supplementary Information for species codes (Supplementary Table 1).*

for the fourteen most-common species (accounting for 72% of trees in the plot ≥ 1cm DBH and 92% ≥ 10cm DBH) measured at four-year intervals using 20 years (1992–

2012) of growth records on 9015 trees (see Methods). There was a high variability in growth patterns across species (Supplementary Fig. 1), which led to contrasted uptake parameters (Supplementary Fig. 3). We simulated species-specific time series of mean depth of water-uptake (Uptake-Depth) (see Methods, Supplementary Fig. 4). Uptake depths averaged over 20 years (Uptake-Depth_{20yr}, Fig. 2a) were below the soil zone (2m) for all species and spanned a broad range of distinct values with some species uptaking water at more than 15m, demonstrating that the fourteen common tree species partitioned hydrological niches in vertical space (Supplementary Fig. 5). The four co-dominant species—accounting for 50% trees ≥ 1cm DBH and 73% ≥ 10cm DBH and, hence, expected to be in strong competition for the critical resource of water—displayed clearly distinct Uptake-Depths_{20yr}, confirming the hypothesis that competition drives hydrological niche separation. Uptake-Depths_{20yr} did not systematically vary with stem size (Supplementary Fig. 6), which is understandable given that in this fire-prone forest rooting depths may be similar between small and large trees: here, small stems alternate between being "top-killed" under frequent low-intensity ground fires, followed by re-sprouting—a cycle that may continue for several decades before stems become large enough (>5-10cm DBH) to escape the fire trap by which stage they will have had the opportunity to develop deep roots (Sukumar *et al.* 2005; Mondal & Sukumar 2015). As expected, canopy species with deeper Uptake-Depth_{20yr} showed decreasing correlation of growth with rainfall (Supplementary Fig. 7). The estimated shallow Uptake-Depth_{20yr} for *T. grandis* is consistent with the scarce maximum rooting depth observations available (Stone & Kalisz 1991) and it being one of the few species with dendro-climatological potential in the tropics. The dynamics of annual water-uptake depths (Fig. 2b) demonstrated the importance of temporal hydrological niches on the long-term: species foraged water at more or less constant depths, except during drought where divergence revealed differential species strategies (see, especially 2001). In the exceptionally dry period of 2002–2003 most species Uptake-Depths_{annual} became shallower, as expected because the deep vadose zone dried up.

Does uptake depth explain drought driven mortality across species? We explored this only for the six most abundant canopy species (accounting for 54% of trees ≥ 1cm DBH and 79% ≥ 10cm DBH), as mortality rates due to natural causes are very low in this forest (Suresh, Dattaraja & Sukumar 2010) and large sample sizes are necessary for detecting a response (See Methods and Supp. Info.). Mortality rates for some species peaked in some years, especially in 2004, just after the end of the exceptional drought period (Supplementary Fig. 8). We tested species vulnerability to the 2000–2003 dry period by comparing mortality rates in 2004 with predrought mortality rates (1997-

1999), and found that drought-driven mortality dramatically increased with 20-yr average uptake depth, especially when compared with the uptake depth in the drought year 2001 (Fig. 3).

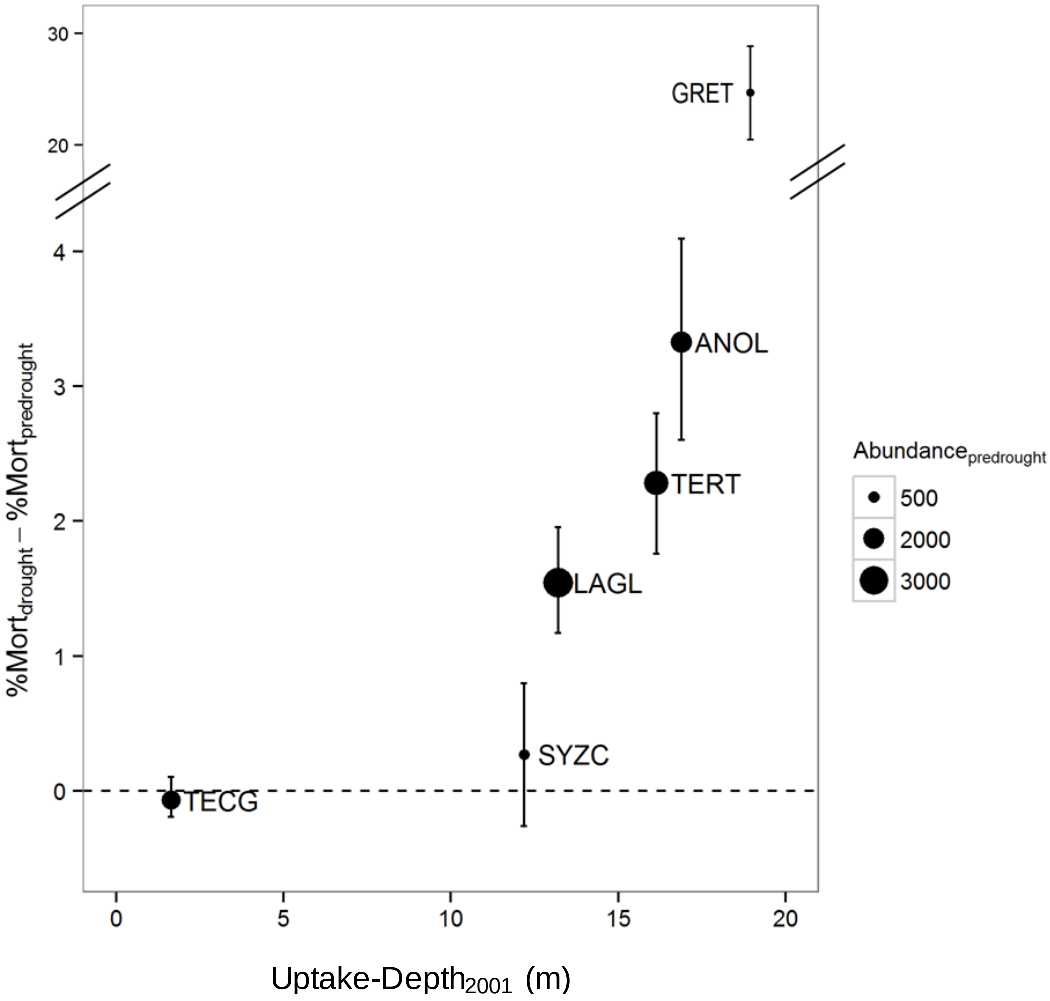


Figure 3 | Increase in mortality during extreme drought as a function of species Uptake-Depth$_{2001}$. *Difference in species drought (2004) and predrought (mean, 1997-1999) per cent mortality rate are plotted against species annual water-uptake depth (mean across size classes) for the moderate drought year 2001, the year for which there was greatest divergence in species water-uptake depths during the prolonged drought from 2000-2003. Results were similar when %Mort$_{Drought}$ was based on cumulative mortality over 2000-2003 (not shown). Error bars are 95% bootstrapped CI for %Mort$_{Drought}$. Only canopy species with tree numbers in 2003 (Abundance$_{predrought}$) greater than 300 in the 50 ha MFDP are plotted. Symbol size is proportional to species Abundance$_{predrought}$. Only trees greater than 5 cm DBH (diameter at breast height) were included for mortality rate calculation. See Supplementary Information for species codes (Supplementary Table 1).*

This may seem a counter-intuitive result, as tree deep-rootedness is commonly associated with drought-resilience (Poorter 2005), but the result is consistent with our hydrological model, however, as it projects prolonged water scarcity at these depths over this period. This suggests that trees specialised in deep water-uptake may, in fact, be poorly adapted to exceptional droughts that may have multi-decadal return times. Our water-stress model further suggests that trade-offs between growth and mortality operate differently depending on species uptake depths (Fig. 4). Species with deep Uptake-Depth$_{20yr}$ are consistently close to their growth potential across most of the years, but show high stress and higher mortality, when the deep water resources become unavailable. Conversely, species with shallow Uptake-Depth$_{20yr}$ are always under stress—far from their growth potential—but show less stress and no decline in survival during the long drought years, by making use of available shallow water or perhaps other strategies such as becoming dormant. This highlights the fact that it is the species-specific "experienced" drought that matters for demography and not meteorological drought.

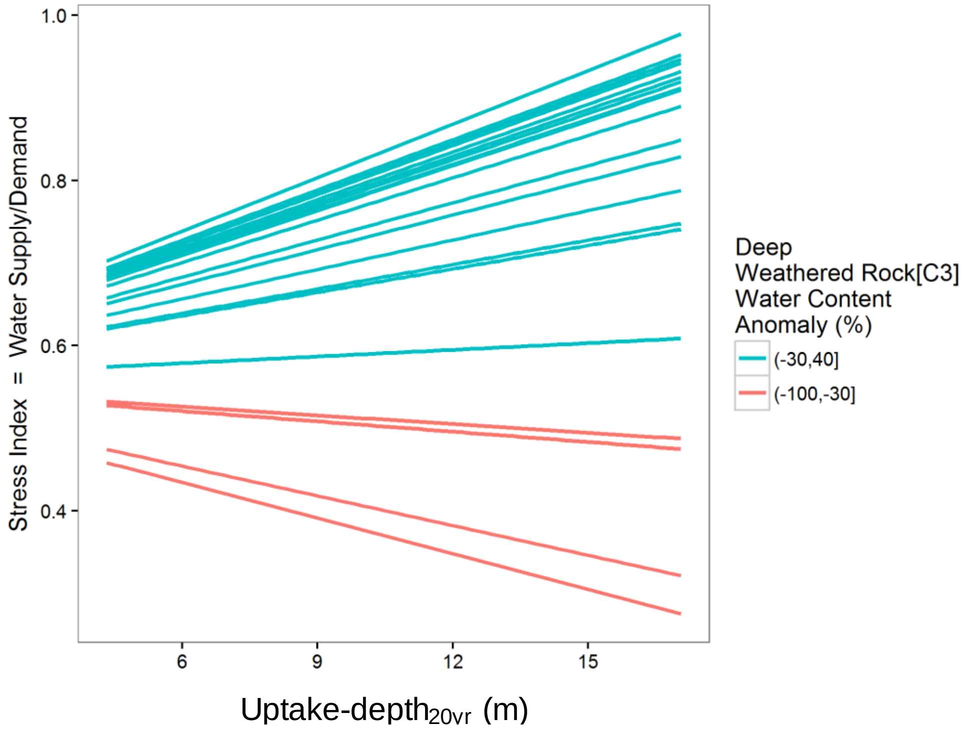
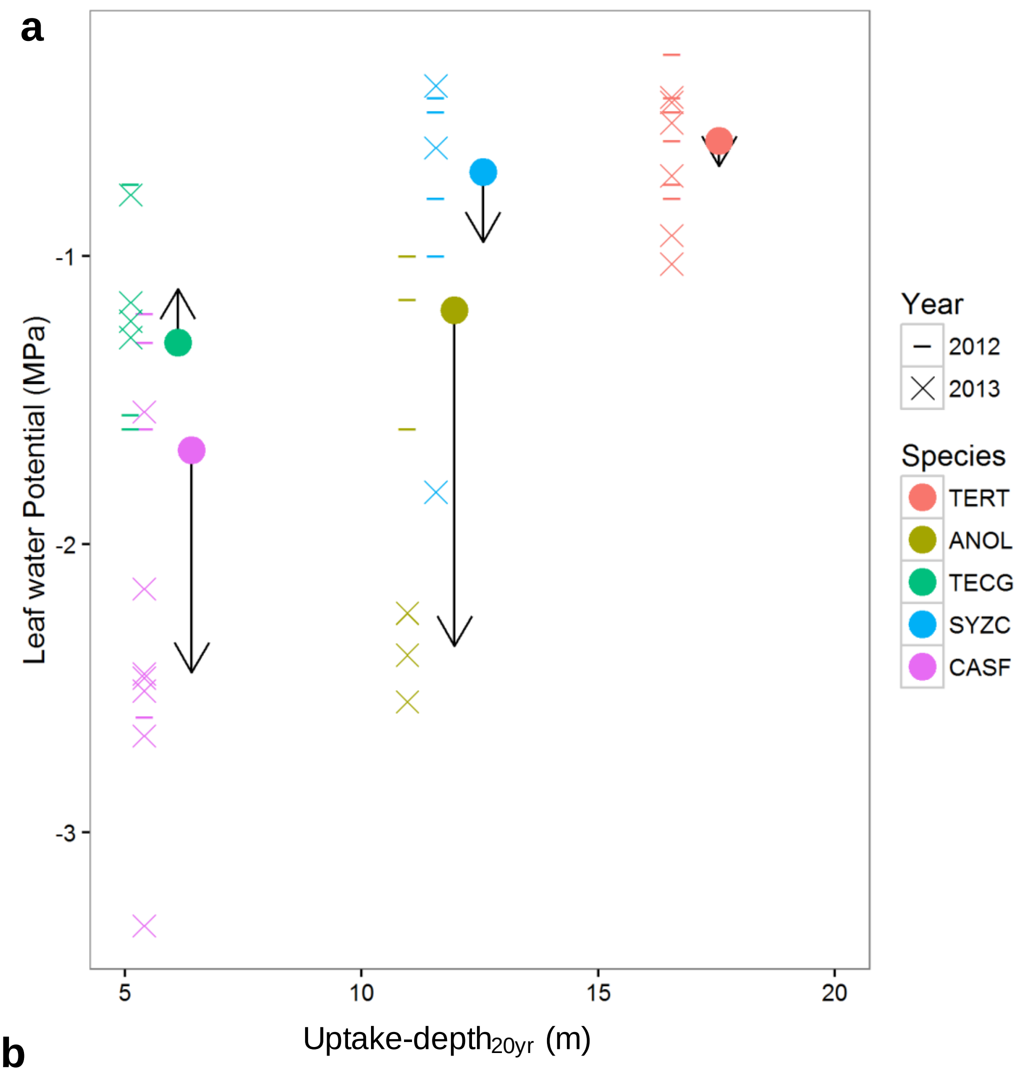


Figure 4 | Illustration of how species Stress Index (supply-to-demand ratio of evapotranspiration) varies with species Uptake-Depth$_{20yr}$ depending on the drought severity of the year. *For each year from 1992–2012, species Stress Index predicted from the water-stress model is calculated along with species Uptake-Depth$_{20yr}$ (mean across size classes). For this illustration species Uptake-Depth$_{20yr}$ is then regressed on species Stress Index, using a linear mixed effects model, with a random intercept and slope for grouping variable year (N = 280; Years (grouping factor) = 20). Predictions from this model for each year are presented as a function of Uptake-Depth$_{20yr}$, color coded by percent Deep Weathered Rock [C3] zone water content anomaly for that year.*

Interestingly, Uptake-Depth$_{20yr}$ was not correlated with species position on the isohydry-anisohydry axis (as approached based on species minimum leaf water potential (ψ_{min}) and variations across two contrasted dry seasons; see Methods, Fig. 5). Species showing large differences in Ψ_{min} are likely to have seen large differences in water availability across the two dry seasons and are likely to be anisohydric. Such species (CASF, ANOL) were found to span shallow to deep Uptake-Depths$_{20yr}$ (Fig. 5a). Species that did not show variations in Ψ_{min} were also found to be with shallow (TECG) or deep Uptake-Depths$_{20yr}$ (TERT). Simulated difference in water availability across the two dry seasons showed that only the C2 compartment decreased in water content post-drought, while soil (C1) remained equally dry, and C3 compartment remained full (Fig. 5b). Combining these results with Ψ_{min} measurements suggests that stable Ψ_{min} could be found either for species with isohydric strategy (TECG) or having similar water availability across years (TERT).

Variation in Uptake-Depth$_{annual}$ with drought, however, was positively correlated with variation in Ψ_{min} (Supplementary Fig. 9), suggesting that capacity to forage deeper during the drought is linked to hydraulic traits governing Ψ_{min}. If Uptake-Depth$_{20yr}$ and isohydry-aniosohydry are in fact orthogonal axes in the trait-space characterising drought response, there would be greater opportunities for coexistence by combining traits and strategies both above and below-ground. We propose that species water-uptake depths should be explored within a broader, more comprehensive approach to species-specific drought hardiness. If there is an apparent lack of a link between drought events and mortality, this should not be taken as evidence that a species is 'drought tolerant' unless it is demonstrated that it actually experienced the drought. Trait analyses must therefore include estimate of species-specific "experienced" drought to truly link strategy to demographic outcome. Thus, we call for a re-consideration of the manner in which drought status is assessed and assigned to a species. Our water-stress model that estimates dynamics of plants' actual water-uptake depths vis-à-vis water-availability paves the way for this.

We claim that no adequate experimental method is currently available to directly validate our approach for estimating uptake depths for such a large range of species in natural biodiverse forests, where water-uptake depths can span several tens of meters. Direct observations of rooting systems with pits are not only extremely difficult to make at such depths, but these observations cannot describe the properties responsible for water-uptake: unlike nutrient uptake which needs high root density, effective water-uptake can be secured by very few roots, easily missed by observations. On the contrary, presence of roots does not imply that they significantly contribute to water-uptake (Meinzer, Clearwater & Goldstein 2001). Indirect methods (e.g. using



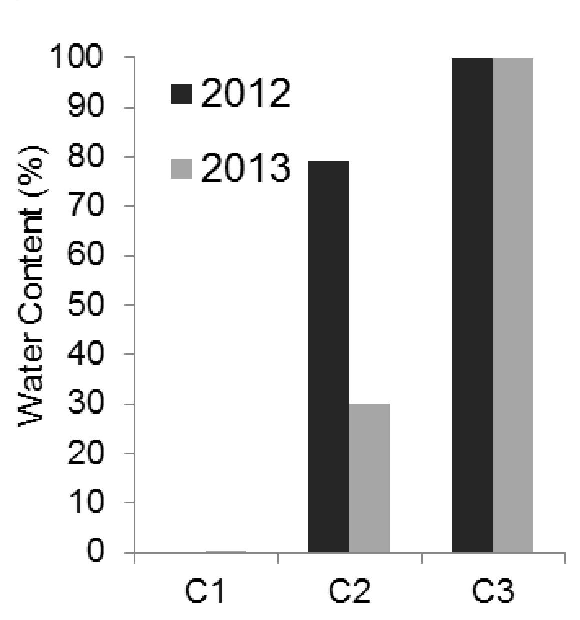


Figure 5 | Species Uptake-Depth$_{20yr}$ versus Ψ$_{min}$ across two dry seasons separated by a drought year. a, *Species Uptake-Depth$_{20yr}$ vs individual tree Ψ$_{min}$ (dry season, midday leaf water potential) for year 2012 (dash) and 2013 (cross) by species. Mean Ψ$_{min}$ (solid point) for dry season 2012, and change in mean Ψ$_{min}$ (arrow) for dry season 2013 are shown against species Uptake-Depth$_{20yr}$ +1 for clarity. Ψ$_{min}$ was measured for three to seven trees (mean = five) of each species in each year on sunlit, mature leaves.* ***b,*** *Water content (per cent of the compartment maximum water content) in C1 (soil), C2 (shallow-weathered rock) and C3 (deep-weathered rock) compartments, as estimated by model COMFORT in dry season 2012 and 2013 for the same periods in which Ψ$_{min}$ were measured***.** *See Supplementary Information for species codes.*

stable isotopes or other tracers) are more meaningful to estimate the depth of water-uptake: however, methods based on natural isotopic abundance are mostly limited to shallow root systems (Silvertown *et al.* 2015) as the isotopic gradient especially in the tropics is largely due to evaporative fractionation (Meinzer *et al.* 2001), which is limited to top soil horizons. Experiments with enriched tracers are impractical at such depths and for hyper-diverse species communities. Most importantly they provide only "snapshots" at a given period, unable to reveal crucial dynamics of species water-uptake depths.

However, the approach is indirectly validated by the consistency between the species-rankings for Uptake-Depths$_{2001}$ and the species-rankings of mortality in the exceptional drought (Fig. 4) and the variation in Uptake-Depths$_{annual}$ through drought being strongly linked to variation in Ψ_{min} (Supplementary Fig. 9). This model therefore offers a unique way to estimate belowground processes that are important to inference about community response to droughts which would otherwise remain completely unknown.

To our knowledge this is the first time a mechanistic link between hydrological niche separation and tree demography has been documented for a diverse tropical forest community. We have shown that, for the long-lived forest trees, hydrological niche dynamics play out over decades through interaction with a deep vadose zone. The depth of the ecosystem, underestimated by virtually all models dealing with vegetation-climate interactions, lends the eco-hydrological system a long memory for past climate patterns and cyclical rainfall variation with seasonal, supra-annual, decadal (like ENSO or IOD) and perhaps even longer return times. We expect such mechanisms to be globally significant, as deep rootedness is increasingly found to be ubiquitous across seasonally dry, semi-arid to humid regions under vegetation types as varied as savanna, thorn-scrub, seasonally deciduous, and evergreen forests (Schenk & Jackson 2002; Ohnuki *et al.* 2008; Schwinning 2010). These mechanisms might have played a significant role in drought-driven changes in composition and function that have been demonstrated in Amazonian (Doughty *et al.* 2015), African (Phillips *et al.* 2010), and south-east Asian (Van Nieuwstadt & Sheil 2005) tropical forests and savannas (Fensham, Fairfax & Ward 2009), as well as in temperate and boreal forests (Ma *et al.* 2012). Exploring these mechanisms has become even more important as climate is changing in mean state as well as in variability, with projected increase in drought frequency and intensity (IPCC 2013) that can change the specific frequency in patterns of water availability that each tree species is adapted to. We call for a gathering of existing, long-term forest demography and hydrological datasets across the globe to be synthesised in the proposed analytical framework to better understand species-coexistence across forest types and improve mechanistic predictions of productivity and compositional change under future drought.

Methods

Demographic data

We used growth and mortality data from the 50 ha Forest Dynamics Plot (11°35′N, 76°32′E) in Mudumalai National Park (MFDP). The MFDP is seasonally dry tropical forest situated along a rainfall gradient in the rain shadow of the Western Ghats mountain range in India. Annual rainfall at the MFDP is 1200 ± 280 mm (mean ± SD for 1988–2013), 70% of which is received during the summer monsoon (June-September). At the MFDP, every woody stem above 1 cm DBH has been tagged with a unique number, identified to species or morpho-species level and mapped (Sukumar *et al.* 1992; Condit *et al.* 2014). Every 4 years, from 1988 to 2012, each woody stem was re-measured. Mortalities and recruitment (stems entering the ≥ 10 mm DBH class) were recorded every year from 1989 to 2008 and cause of mortality—fire, herbivory by large mammal such as elephants, or other causes—was recorded.

For growth data, we selected from MFDP the set of trees (above 10 mm DBH) that were alive from 1992 to 2012 with DBH data available throughout this period and were single stemmed. We did not use growth data from 1988–1992 as reliable rainfall data at MFDP for this period was not available (see Hydrological data). The selected trees constituted nearly half of the trees ever recorded in the plot from 1992 to 2012. Trees that did not match these criteria were mostly small trees that were present in only one or a few censuses. Individual tree growth rate ($cm.yr^{-1}$) was calculated as the difference between DBH measured in successive censuses, divided by the inter-census interval. We removed from analyses those trees (n = 110) with "spike" growth rates—those greater than two standard deviations from the mean growth rate of a tree over all census intervals. With distribution of mean tree growth rates across censuses being 0.2 [0.05 – 0.6; 5 – 95 percentiles] $cm.yr^{-1}$ we also considered growth rates below -0.5 $cm.yr^{-1}$ and greater than 1.5 $cm.yr^{-1}$ in any given census as erroneous and removed those trees (n = 361) from the analysis. Only species with greater than 100 trees each in the selected set were retained for analyses. In total, analyses were performed on 9015 trees belonging to 14 species. Four species – *Lagerstroemia microcarpa* Wt., *Terminalia crenulata* Roth., *Tectona grandis* L. f., *Anogeissus latifolia* (Roxb. ex DC.) Wall. ex Guillem. & Perr. – nearly co-dominantly constitute more than half of the trees in the MFDP (mean across all censuses: 50% of ≥ 1 cm DBH, 73% of ≥ 10 cm DBH trees). These 14 species together constitute more than three-quarters of the trees in the

MFDP (mean across all censuses: 72% of ≥1 cm DBH, 92% of ≥ 10 cm DBH trees) and, given such a high representation in the large size class, they almost completely account for the above-ground biomass in the MFDP. Quantile-based size classes were constructed within species—five each for the four co-dominant species, and three each for the rest. Time series of mean growth rates for each size class by species were used for further analyses (n = 13 to 441 per size class depending on species, see Supplementary Table 2).

Hydrological data and model

Except phreatophytes that have specialized anatomical features allowing root growth and water-uptake in low oxygen, water-saturated environments (Orellana *et al.* 2012), trees can only access water from the vadose zone (unsaturated zone from the top soil to the groundwater table). Belowground water availability in the vadose zone was simulated using the hydrological model COMFORT (Ruiz *et al.* 2010)—a conceptual water balance model for forested catchments, calibrated and validated at the Mulehole (11°44′N, 76°27′E) catchment (Descloitres *et al.* 2008; Braun *et al.* 2009; Riotte *et al.* 2014) in Bandipur National Park, c. 25 km away from the MFDP. Annual rainfall at Mulehole is 1095 ± 236 mm (mean ± SD for 1988–2013) and annual PET is 980 ± 64 mm (mean ± SD for 2004–2010). This dynamic model balances the observed incoming rainfall against stream discharge, evaporation from the soil, transpiration of vegetation (as a single leaf model) from soil and weathered-rock zones, recharge of these zones and the water table (see Ruiz *et al.* 2012 for details). To allow for greater variation in water availability by depth, in this work we modified the hydrological model from having two compartments in the vadose zone—soil and weathered bedrock—to three, by splitting the latter into two compartments of equal maximum water content (C2 and C3). The model was run using daily rainfall time series (from 1970 through 2014) at Mulehole and was recalibrated using observations (from 2003 through 2014) of stream discharge and water table levels (Supplementary Fig. 2). Throughout the simulation period, groundwater table level was always deeper than 30 m i.e. the vadose zone was always thicker than 30 m. The thickness of each compartment was estimated based on COMFORT calibrated maximum water content for soil (179.2 mm; $M_{Soil}max$) and weathered bedrock compartments (195.6 mm for C2 and C3; $M_{C2}max$ and $M_{C3}max$), and Available Water Capacity for soil (10 $m^3.m^{-3}$) (Parate *et al.* 2011) and the weathered bedrock (average of 1 and 4 $m^3.m^{-3}$ for weathering class IV or V) (Jones & Graham 1993; Braun *et al.* 2009). The COMFORT model was run for the MFDP by substituting daily rainfall time series from the nearest rain-gauge station—Kargudi (4 km from MFDP)—to obtain a running estimate of daily water availability for each compartment (Supplementary Fig. 2). Thickness of each compartment was assumed to be similar to

Mulehole. Rainfall data at Kargudi were available from 1989, and therefore only the 1989–2014 time series was substituted. However, to avoid initialization inaccuracies, in further analyses, model outputs of water availability at Kargudi were used only from 1992 onwards.

Dynamic model of water-stress on growth

We developed a new dynamic model that assumed deviation from growth potential to be a function of water-stress index (water supply-to-demand ratio). Water supply was assumed to be a function of daily water availability in each belowground compartment at MFDP (M_{Soil}, M_{C2} and M_{C3}; Supplementary Fig. 2) and six uptake parameters varying with species-size class and assumed to be constant though time. These parameters represented rooting density in each of the compartments (R_{Soil}, R_{C2}, R_{C3}; Range 0-1) and the hydraulics: restriction in uptake with depletion of compartment water content (δ_{Soil}, δ_{C2}, δ_{C3}; Range 0-2). Water demand (maximum evapotranspiration [MET]) was determined on a daily basis by a curve of Leaf Area Index and potential evapotranspiration (PET) that was seasonally varying, but was fixed across years (Ruiz *et al.* 2010) ($MET = \varepsilon \text{ x } PET$, where $\varepsilon = 1 - e^{-0.5 \text{ x } LAI}$) and across species-size class, since leaf phenology varies within a narrow range across species in this dry deciduous forest (Prasad & Hegde 1986). The LAI curve was built from literature, corroborated (Prasad & Hegde 1986) by MODIS data and varied as such: from day 31 to 121 of the year LAI remains 0; from day 32 to 211 LAI linearly increases from 0 to 7; then remains static at 7 until day 335; after which linearly decreases to 0 by day 31 of the next year. This demand was supplied on a daily basis from successively deeper compartments depending on availability of water ($T = T_{Soil} + T_{C2} + T_{C3}$, where T = total evapotranspiration, T_{Soil} = minimum $\{M_{Soil}; MET \text{ x } R_{Soil} \text{ x } (M_{Soil}/M_{Soil}max)^{\delta S}\}$, T_{C2} = minimum $\{M_{C2}; (MET\text{-}T_{Soil}) \text{ x } R_{C2} \text{ x } (M_{C2}/M_{C2}max)^{\delta C2}\}$, T_{C3} = minimum $\{M_{C3}; (MET\text{-}T_{Soil}\text{-}T_{C2}) \text{ x } R_{C3} \text{ x } (M_{C3}/M_{C3}max)^{\delta C3}\}$).

Water-stress model inversion to estimate mean depth of water-uptake

A time series of stress index ($\Sigma_{\mathrm{4years}}T/\Sigma_{\mathrm{4years}}MET$) was generated for each species-size class from 1992–2012, using uptake parameters that maximised correlation (Pearson's product-moment correlation coefficient, *r*) with corresponding time series of observed growth rate, after standardizing both time series to range from -1 to +1. These best fitting uptake parameters (R_{Soil}, R_{C2}, R_{C3}, δ_{Soil}, δ_{C2}, δ_{C3}) were estimated (Supplementary Fig. 3) using Generalized Likelihood Uncertainty Estimation (GLUE) (Beven & Binley 1992) (with 10,000 parameter ensemble generated by Latin Hypercube Sampling (McKay, Beckman & Conover 2000). GLUE searches a set of best fitting parameters from the parameter space such that they together maximize the likelihood function (in this case R-sq). The method relies upon absence of equifinality i.e. the absence of many different parameter sets within a chosen model structure that may be behavioural or acceptable in reproducing the observed behaviour of that system. I the present study parameter space was well constrained for almost all the species-size groups i.e. equifinality issue was absent allowing for confidence in the best fitting parameter set chosen (Supplementary Fig. 9). Uptake-Depth for each species-size class was calculated as the average per cent water-uptake from each belowground compartment over a period (e.g. daily, annual, 20 years), weighted by the mean depth of the compartment, so for over a period t, Uptake-Depth$_t$ = $\sum_i^t 1/T \times \{T_{Soil\ i} \times D_{soil} + T_{C2i} \times D_{C2} + T_{C3i} \times D_{C3}\}$, where $D_{soil,}$ D_{C2} and D_{C3} are mean compartment depths.

Statistical analyses

We tested whether species partitioned niches for belowground water as a result of competition. Niche overlaps for all species pairs were calculated using the d-statistic/Chzechanowski Index based on species associations[40] with each belowground compartment—the ratio of a species relative use of a compartment (mean water-uptake across all size classes) and relative water availability in that compartment over 1992–2012. Mean community overlap and all pairwise overlaps were compared against their respective null distributions based on 10,000 pseudo-communities obtained by allowing the niche position and breadth of each species to vary randomly (Gotelli & Graves 1996; Silvertown *et al.* 1999). Mean community niche overlap was significantly lower than the null expectation (observed mean community d-statistic = 0.52, $P < 0.001$; Supplementary Fig. 5a). Niche overlaps for half of the species pairs were significantly lower than their respective nulls (56 out of 105 species pairs with a One-tailed test). We also analysed how niche overlap between species pairs decreased with increasing distance from neighbour in niche space. Within the observed and simulated pseudo-communities, nearest neighbours in niche space were ranked for each species, and mean niche overlap was calculated for each rank across all species (Supplementary Fig. 5b). Although close neighbours (1–4) had highly overlapping niches, onwards to the fifth nearest neighbour observed overlaps were significantly lower than the overlaps predicted under the null model of no niche separation (Inger & Colwell 1977; Winemiller & Pianka 1990). Results were similar when the niche overlap d-statistic was calculated based on the geometric mean (Gotelli & Graves 1996) of associations for each belowground compartment and relative water availability in that compartment over 1992–2012.

To assess species mortality in response to extreme drought as a function of water-uptake depth, we compared difference in species per cent mortality rate in year 2004 (following the extreme drought of 2001–2003) from species predrought mortality rates with species Uptake-Depth$_{2001}$, a year for which divergence in species Uptake-Depth$_{\text{annual}}$ was largest. For species *i*, %Mort$_{\text{Drought}}$ = No. of trees dead$_{2004}$/No. of trees present$_{2003}$ x 100, %Mort$_{\text{Predrought}}$ = mean (No. of trees dead$_{\text{year2}}$/No. of trees present$_{\text{year1}}$ x 100) over 1997 to 1999 (see Supplementary Table 3 and 4). Mortalities recorded as due to causes other than fire or large mammal herbivory alone were included. Results were similar with various tree size restrictions (above 1, 5, 10, or 20 cm DBH). We restricted analyses to canopy species for which tree numbers in 2003 were greater than 300. Species with sample sizes lower than 300 had high uncertainties in their %Mort$_{\text{Drought}}$ estimates based on bootstrapped CIs.

Additional data and analyses

We tested and found (results not shown) that species Uptake-Depth$_{20\text{yr}}$ was not very sensitive to the shape of LAI curve. We also ran a sensitivity analysis to test whether Uptake-Depth$_{20\text{yr}}$ estimation was similar when the growth time series was used at annual or a four-year time scale. For this, we used a master tree-rings based growth time series (1988-2012) developed at Mulehole for *Tectona grandis* L. f. (see Supplementary Information), one of the few species in the study area that can be reliably used for dendrochronology (Jacoby & D'Arrigo 1990). With uptake parameters estimated from the inversion of the water-stress model of water-stress on growth data and COMFORT outputs at Mulehole, we found that Uptake-Depth$_{20\text{yr}}$ estimates were similar for both annual (5.2 m) or 4-year scale (3.2 m) time series of growth and that of stress index ($\sum_{1\text{year}}T/\sum_{1\text{year}}MET$ or $\sum_{4\text{years}}T/\sum_{4\text{years}}MET$) (Supplementary Fig. 4). Stress Index (water supply-to-demand ratio) explained 63% (n = 24, P < 0.01) variation in growth rates (linear regression) when model was run at the annual scale, and 52% (n = 24, P < 0.01) when ran at the four-year scale. Variation in growth was explained well at lower (0%-75%) values of Stress Index, but not at higher values (>75%) of Stress Index (Supplementary Fig. 4). Here water may be the most limiting factor for growth, but at greater levels of water availability growth is probably co-limited by variability in other factors such as light and nutrients. To validate the water-stress model, we also performed exhaustive jack-knife cross-validation tests on both annual and 4-year scale tree-ring based growth time series. The model was able to predict omitted values well (cross-validation RMSE: 0.57 at annual scale and 0.0042 at 4-year scale).

Relationship between minimum Leaf Water Potential and rooting strategies

The current framework to understand drought tolerance is by positioning species on isohydry/anisohydry axis, where anisohydric species maintain stomatal conductance by allowing the leaf water potential (Ψ_{min}) to become more negative, while isohydric specie maintain less negative Ψ_{min} by decreasing stomatal conductance. Here, we measured variations in Ψ_{min} (dry season, midday) using a PMS pressure chamber in 6 species (3-7 individuals [mean = 5] with 2 leaves each) across two dry seasons (February 22nd to 27th, 2012; Jan 2nd, 2013), with the monsoon in year 2012 having a negative rainfall anomaly (-30%, Supplementary Fig. 2).

All analyses was performed using the R statistical platform, version 3.2.2 (R Core Team 2015).

Acknowledgements

The Mudumalai FDP program is funded by Ministry of Environment and Forests, Govt. of India. The Mulehole catchment environmental observatory is part of the ORE-BVET project (Observatoire de Recherche en Environnement – Bassin Versant Expe´rimentaux Tropicaux - http://bvet.omp.obs-mip.fr/index.php/eng/ - supported by the French Institute of Research for Development (IRD), CNRS-INSU and Toulouse University. We thank Tamilnadu and Karnataka Forest Departments for permissions to work at Mudumalai and Bandipur National Parks, respectively, and their field staff for logistic support. We thank numerous field assistants and staff at Centre for Ecological Sciences, Bangalore and Indo-French Cell for Water Sciences, Bangalore (IFCWS) for field work and logistic support over the last three decades. R.C.T. was supported by CSIR, India doctoral student fellowship and by an IRD grant to IFCWS. L.R. was deputed to IFCWS on an IRD Fellowship. R.S. was a J. C. Bose National Fellow during the period of this study. Funding was also provided to S.M.M. through NSF grant (1137366). An NSF grant to the Smithsonian Institution's Center for Tropical Forest Science-Forest Global Earth Observatory (Dimensions 1046113) also partially supported this study through R.C.T. and S.M.M. Comments by Susanne Schwinning improved this manuscript.

References

Allen, C.D., Breshears, D.D. & McDowell, N.G. (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, **6**, 1–55.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H. (Ted), Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J. -H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management, 259, 660–684.

Anderegg, L.D.L., Anderegg, W.R.L. & Berry, J.A. (2013a) Not all droughts are created equal: translating meteorological drought into woody plant mortality. Tree Physiology, 33, 672–683.

Anderegg, W.R.L., Kane, J.M. & Anderegg, L.D.L. (2013b) Consequences of widespread tree mortality triggered by drought and temperature stress. Nature Climate Change, 3, 30–36.

Bennett, A.C., McDowell, N.G., Allen, C.D. & Anderson-Teixeira, K.J. (2015) Larger trees suffer most during drought in forests worldwide. Nature Plants, 1.

Beven, K. & Binley, A. (1992) The future of distributed models: Model calibration and uncertainty prediction. Hydrological Processes, 6, 279–298.

Braun, J.-J., Descloitres, M., Riotte, J., Fleury, S., Barbiéro, L., Boeglin, J. -L., Violette, A., Lacarce, E., Ruiz, L., Sekhar, M., Mohan Kumar, M.S., Subramanian, S. & Dupré, B. (2009) Regolith mass balance inferred from combined mineralogical, geochemical and geophysical studies: Mule Hole gneissic watershed, South India. Geochimica et Cosmochimica Acta, 73, 935–961.

Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martínez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J. & Zanne, A.E. (2012) Global convergence in the vulnerability of forests to drought. Nature, 491, 752–755.

Condit, R., Lao, S., Singh, A., Esufali, S. & Dolins, S. (2014) Data and database standards for permanent forest plots in a global network. Forest Ecology and Management, 316, 21–31.

Descloitres, M., Ruiz, L., Sekhar, M., Legchenko, A., Braun, J. -J., Kumar, M. & Subramanian, S. (2008) Characterization of seasonal local recharge using electrical resistivity tomography and magnetic resonance sounding. Hydrological Processes, 22, 384–394.

Doughty, C.E., Metcalfe, D.B., Girardin, C.A.J., Amézquita, F.F., Cabrera, D.G., Huasco, W.H., Silva-Espejo, J.E., Araujo-Murakami, A., da Costa, M.C., Rocha, W. & others. (2015) Drought impact on forest carbon dynamics and fluxes in Amazonia. Nature, 519, 78–82.

Fensham, R.J., Fairfax, R.J. & Ward, D.P. (2009) Drought-induced tree death in savanna. Global Change Biology, 15, 380–387.

Gotelli, N.J. & Graves, G.R. (1996) Null Models in Ecology. Smithsonian Institution Press, Washington and London.

Inger, R.F. & Colwell, R.K. (1977) Organization of Contiguous Communities of Amphibians and Reptiles in Thailand. Ecological Monographs, 47, 229–253.

IPCC. (2013) Climate Change 2013: The Physical Science Basis. (Eds Stocker et Al.). Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jacoby, G.C. & D'Arrigo, R.D. (1990) Teak (Tectona grandis L.F.), A tropical species of large-scale dendroclimatic potential. Dendrochronologia, 8, 83–98.

Jones, D.P. & Graham, R.C. (1993) Water-Holding Characteristics of Weathered Granitic Rock in Chaparral and Forest Ecosystems. Soil Science Society of America Journal, 57, 256–261.

Kleidon, A. & Heimann, M. (2000) Assessing the role of deep rooted vegetation in the climate system with model simulations: mechanism, comparison to observations and implications for Amazonian deforestation. Climate Dynamics, 16, 183–199.

Ma, Z., Peng, C., Zhu, Q., Chen, H., Yu, G., Li, W., Zhou, X., Wang, W. & Zhang, W. (2012) Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. Proceedings of the National Academy of Sciences, 109, 2423–2427.

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

McKay, M.D., Beckman, R.J. & Conover, W.J. (2000) A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. Technometrics, 42, 55–61.

Meinzer, F.C., Clearwater, M.J. & Goldstein, G. (2001) Water transport in trees: current perspectives, new insights and some controversies. Environmental and Experimental Botany, 45, 239–262.

Meir, P., Mencuccini, M. & Dewar, R.C. (2015) Drought-related tree mortality: addressing the gaps in understanding and prediction. New Phytologist, 207, 28–33.

Mondal, N. & Sukumar, R. (2015) Regeneration of juvenile woody plants after fire in a seasonally dry tropical forest of Southern India. Biotropica, 47, 330–338.

Ohnuki, Y., Shimizu, A., Chann, S., Toriyama, J., Kimhean, C. & Araki, M. (2008) Seasonal change in thick regolith hardness and water content in a dry evergreen forest in Kampong Thom Province, Cambodia. Geoderma, 146, 94–101.

Orellana, F., Verma, P., Loheide, S.P. & Daly, E. (2012) Monitoring and modeling water-vegetation interactions in groundwater-dependent ecosystems. Reviews of Geophysics, 50, RG3003.

Parate, H.R., Kumar, M.S.M., Descloitres, M., Barbiero, L., Ruiz, L., Braun, J.-J., Sekhar, M. & Kumar, C. (2011) Comparison of electrical resistivity by geophysical method and neutron probe logging for soil moisture monitoring in a forested watershed. Current Science, 100, 1405–1412.

Phillips, O.L., van der Heijden, G., Lewis, S.L., López-González, G., Aragão, L.E.O.C., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, Á.C.A., Chao, K.-J., Cardozo, N.D., 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, A., Vargas, P.N., Patiño, S., Peh, K.S.-H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez, H., Rudas, A., Salamão, R., Schwarz, M., Silva, J., Silveira, M., Ferry Slik, J.W., Sonké, B., Thomas, A.S., Stropp, J., Taplin, J.R.D., Vásquez, R. & Vilanova, E. (2010) Drought–mortality relationships for tropical forests. New Phytologist, 187, 631–646.

Poorter, L. (2005) Resource capture and use by tropical forest tree seedlings and their consequences for competition. Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity (eds D. Burslem, M. Pinard & S. Hartley), p. Cambridge University Press.

Prasad, S.N. & Hegde, M. (1986) Phenology and seasonality in the tropical deciduous forest of Bandipur, South India. Proceedings of the Indian Academy of Sciences: Plant Sciences, 96, 121–133.

R Core Team. (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Australia.

Riotte, J., Maréchal, J.C., Audry, S., Kumar, C., Bedimo, J.P., Ruiz, L., Sekhar, M., Cisel, M., Chitra Tarak, R., Varma, M.R.R., Lagane, C., Reddy, P. & Braun, J.J. (2014) Vegetation impact on stream chemical fluxes: Mule Hole watershed (South India). Geochimica et Cosmochimica Acta, 145, 116–138.

Rodriguez-Iturbe, I. (2000) Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamies. Water Resources Research, 36, 3–9.

Ruiz, L., Varma, M.R., Kumar, M.M., Sekhar, M., Maréchal, J.-C., Descloitres, M., Riotte, J., Kumar, S., Kumar, C. & Braun, J.-J. (2010) Water balance modelling in a tropical watershed under deciduous forest (Mule Hole, India): Regolith matric storage buffers the groundwater recharge process. Journal of Hydrology, 380, 460–472.

Schenk, H.J. & Jackson, R.B. (2002) Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. Journal of Ecology, 90, 480–494.

Schwinning, S. (2010) The ecohydrology of roots in rocks. Ecohydrology, 3, 238–245.

Schwinning, S. & Kelly, C.K. (2013) Plant competition, temporal niches and implications for productivity and adaptability to climate change in water-limited environments. Functional Ecology, 27, 886–897.

Silvertown, J., Araya, Y. & Gowing, D. (2015) Hydrological niches in terrestrial plant communities: a review. Journal of Ecology, 103, 93–108.

Silvertown, J., Dodd, M.E., Gowing, D.J.G. & Mountford, J.O. (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature, 400, 61–63.

Skelton, R.P., West, A.G. & Dawson, T.E. (2015) Predicting plant vulnerability to drought in biodiverse regions using functional traits. Proceedings of the National Academy of Sciences, 112, 5744–5749.

Stone, E.L. & Kalisz, P.J. (1991) On the maximum extent of tree roots. Forest Ecology and Management, 46, 59–102.

Sukumar, R., Dattaraja, H.S., Suresh, H.S., Radhakrishnan, J., Vasudeva, R., Nirmala, S. & Joshi, N.V. (1992) Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India. Current Science, 62, 608–616.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Srinidhi, S. & Nath, C. (2005) The dynamics of a tropical dry forest in India: climate, fire, elephants and the evolution of life-history strategies. Biotic Interactions in the Tropics, Ecological Reviews, p. Cambridge University Press.

Suresh, H.S., Dattaraja, H.S. & Sukumar, R. (2010) Relationship between annual rainfall and tree mortality in a tropical dry forest: Results of a 19-year study at Mudumalai, southern India. Forest ecology and management, 259, 762–769.

Van Nieuwstadt, M.G. & Sheil, D. (2005) Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia. Journal of Ecology, 93, 191–201.

Winemiller, K.O. & Pianka, E.R. (1990) Organization in natural assemblages of desert lizards and tropical fishes. Ecological Monographs, 60, 27–55.

Appendix

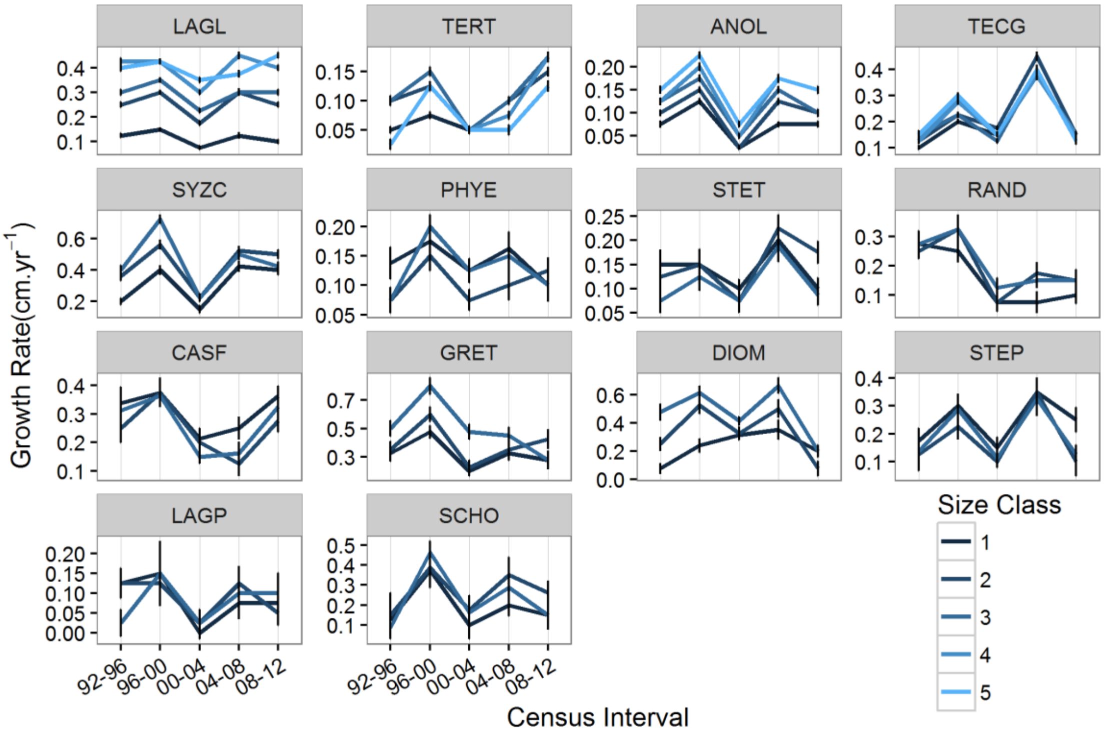
Preparation of Tree Ring time series

From 10 trees (40 +- 8 cm DBH; mean+-SD) of *T. grandis* at Mulehole catchment, we collected about 10 cm long, 5 mm diameter wood cores**.** Using Haglof increment borer 3-5 cores were collected from each tree at 140 cm from tree base at radially symmetric points around the tree circumference. These cores were sanded with successively fine grained silicon carbide sandpapers (P600-P800). Cores were then scanned at 1200 dpi, and ring widths measured using ImageJ software (Schneider et al. 2012). First, we compared and cross-dated ring width time series from multiple cores of each tree. An average growth time series for each tree was then obtained. These were then compared across trees and cross-dated. Cross-dating was done manually, without using COFECHA and without de-trending, for we did not observe any size-dependent trend, and did not want to remove climatic trend, if any. Once cross-dated, we obtained a time series of ring-widths averaged across the ten trees.

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

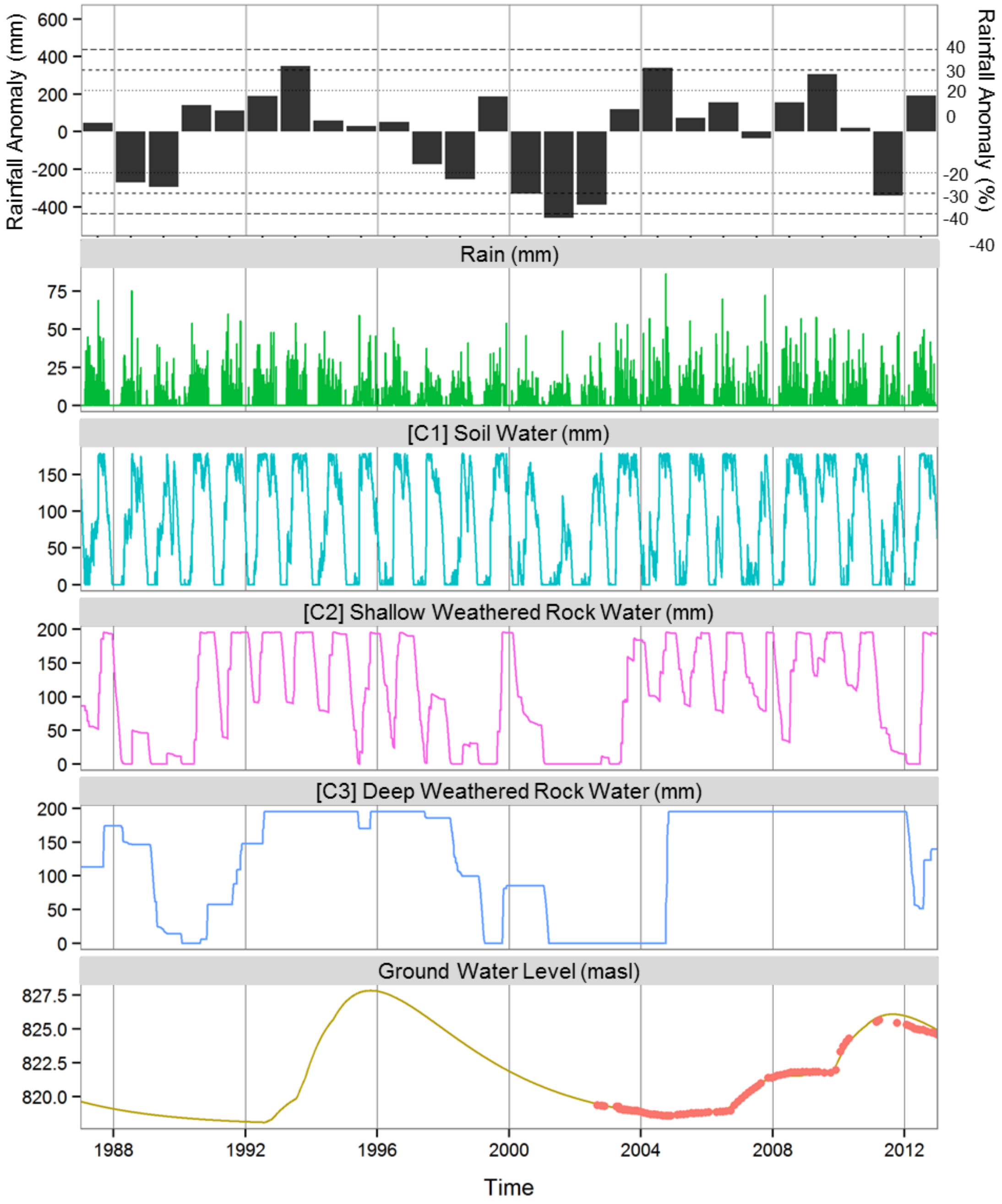
Supplementary Figures:

Supplementary Fig. 1



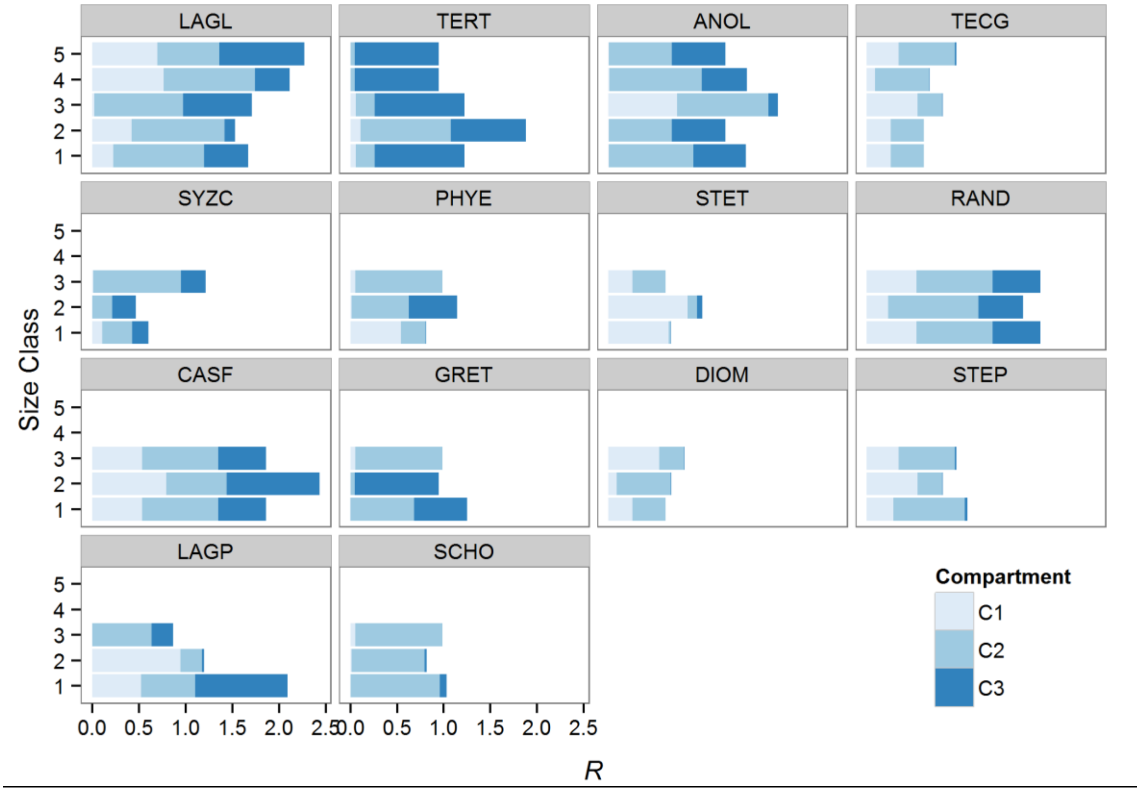
Supplementary Fig. 1 | Time series of mean growth rate (± S.E.M. n= 13 to 441 trees depending on species, see Supplementary Table 2) for each equal quantile based size class within species. See Supplementary Information for species codes (Supplementary Table 1).

Supplementary Fig. 2

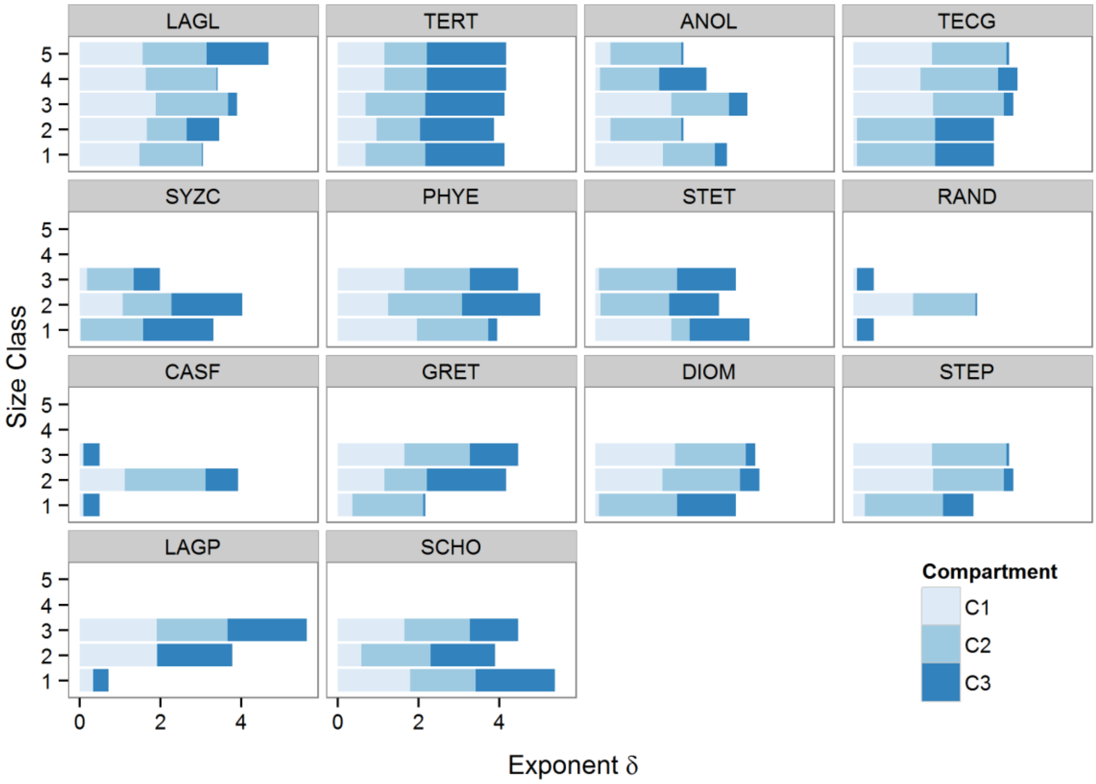


Supplementary Fig. 2 | Belowground water availability as estimated by the hydrological model COMFORT at Mulehole. 1988 to 2013 time series—from top to bottom—of annual rainfall anomaly, observed daily rainfall, simulated water content of three belowground compartments, along with simulated (brown line) and observed (2003-2013, red dots) ground water table level. Grey vertical lines mark Mudumalai growth census year-ends. The bottom of each compartment is estimated to be 2 m, 14 m and 26 m from the surface, respectively. Minimum and maximum water-table levels showns are at 32 to 42 m from the surface, respectively. For 1988-2012, correlations (Pearson's product-moment correlation coefficient, r) between mean annual compartment water content for C1, C2 and C3 and annual rainfall (n = 25 years) were 0.84, 0.79 and 0.23 with P <0.01, <0.01 and 0.3, respectively; and those for monthly rainfall (n 300 months) were 0.55, -0.02 and 0, with P < 0.01, < 0.01 and 0.9, respectively.

Supplementary Fig. 3 a

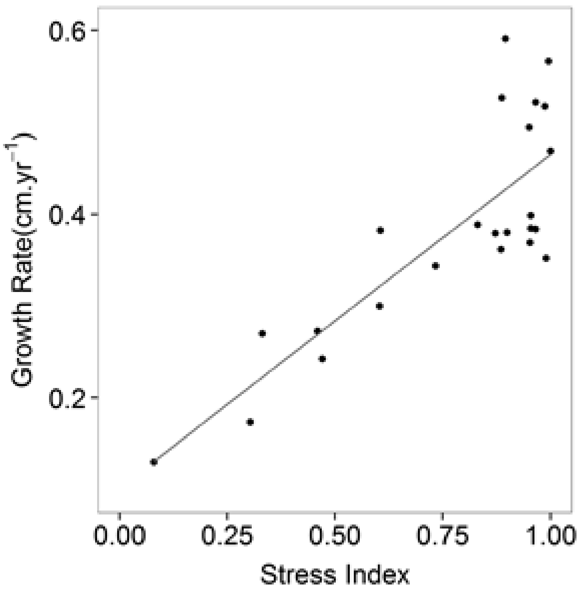


Supplementary Fig. 3 b

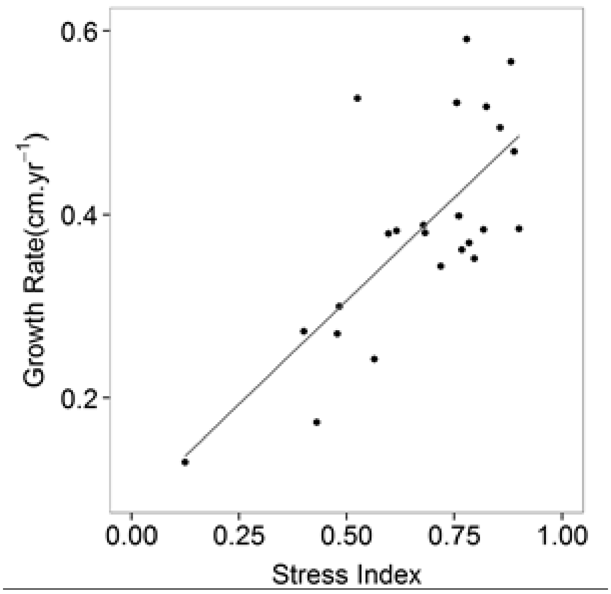


Supplementary Fig. 3 | Stacked bars of model estimated rooting density parameters (Ri) in a and parameters for access restriction with depletion of compartment water content (δi) in b, for soil, C2 and C3 compartments (colour coded) for each species-size group. Size classes are quantiles within species, with size increasing from class 1 to 5. The four co-dominant species have five size classes and other species have three size classes. See Supplementary Information for species codes (Supplementary Table 1).

Supplementary Fig. 4 a

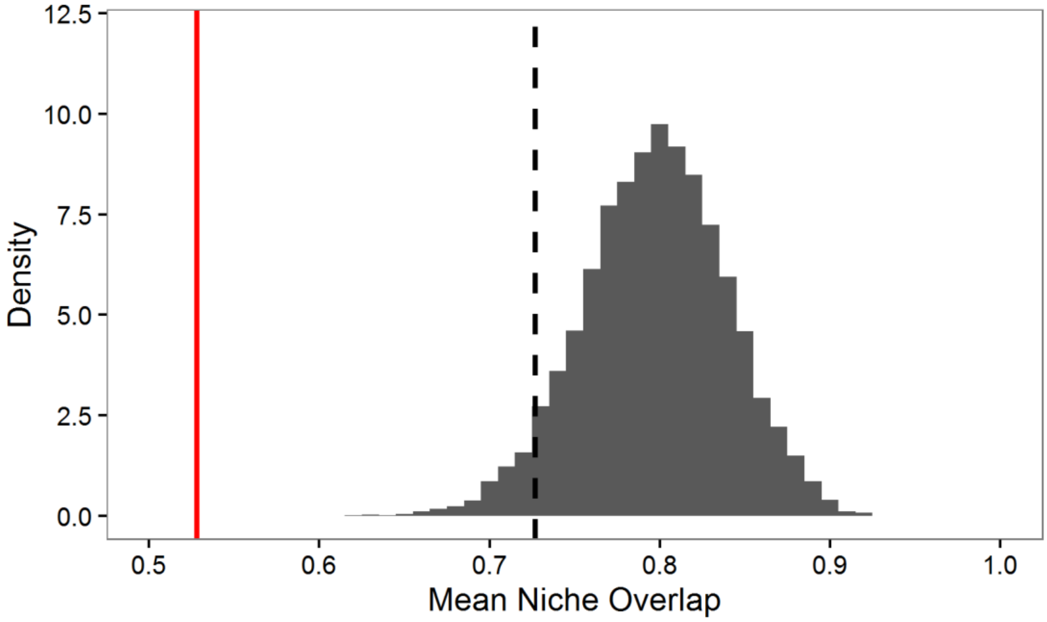


Supplementary Fig. 4 b

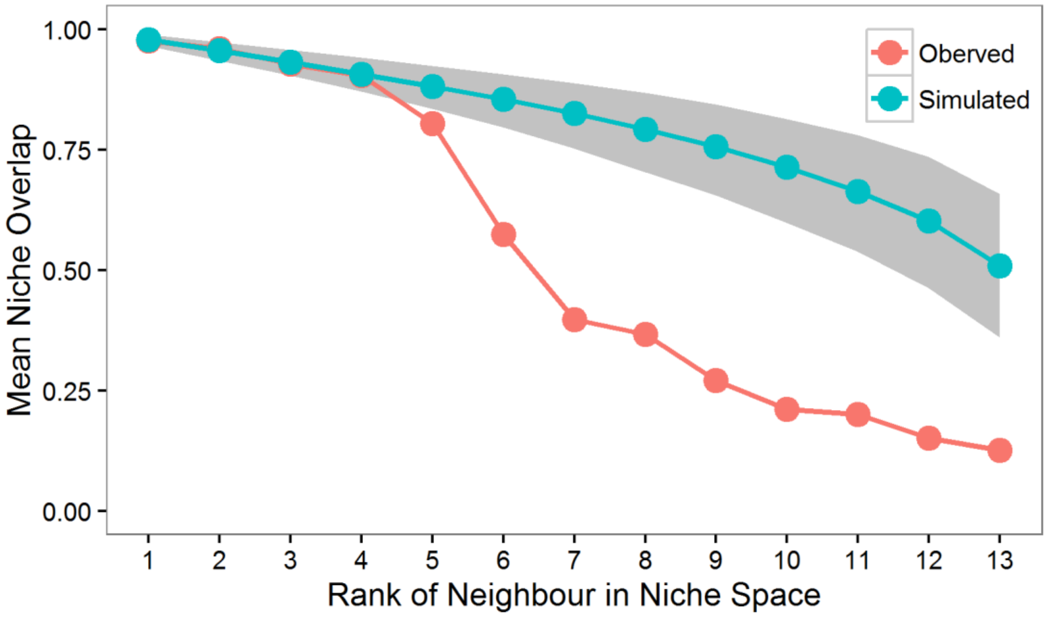


Supplementary Fig. 4 | Tree-rings based observed annual growth for Tectona grandis from 1988-2012 vs. water-stress model estimated annual Stress Index (supply-to-demand ratio of evapotranspiration), when model was run at two different scales: (a) annual and (b) 4-year growth scale. For b best fit uptake parameters for the water-stress model were found for a growth time series obtained by summing up the annual growth time series at 4-year scale. Using these parameters model was re-run at annual scale and Stress Index predictions were obtained. Goodness-of-fit (R^2) values for regressions of annual growth rates against Stress Index were found to be similar at both the scale, with 0.63 for annual scale ($n = 24$, $P < 0.001$) and 0.52, for 4-year scale ($n = 24$, $P < 0.001$). Blue lines depict linear regression curves.

Supplementary Fig. 5a

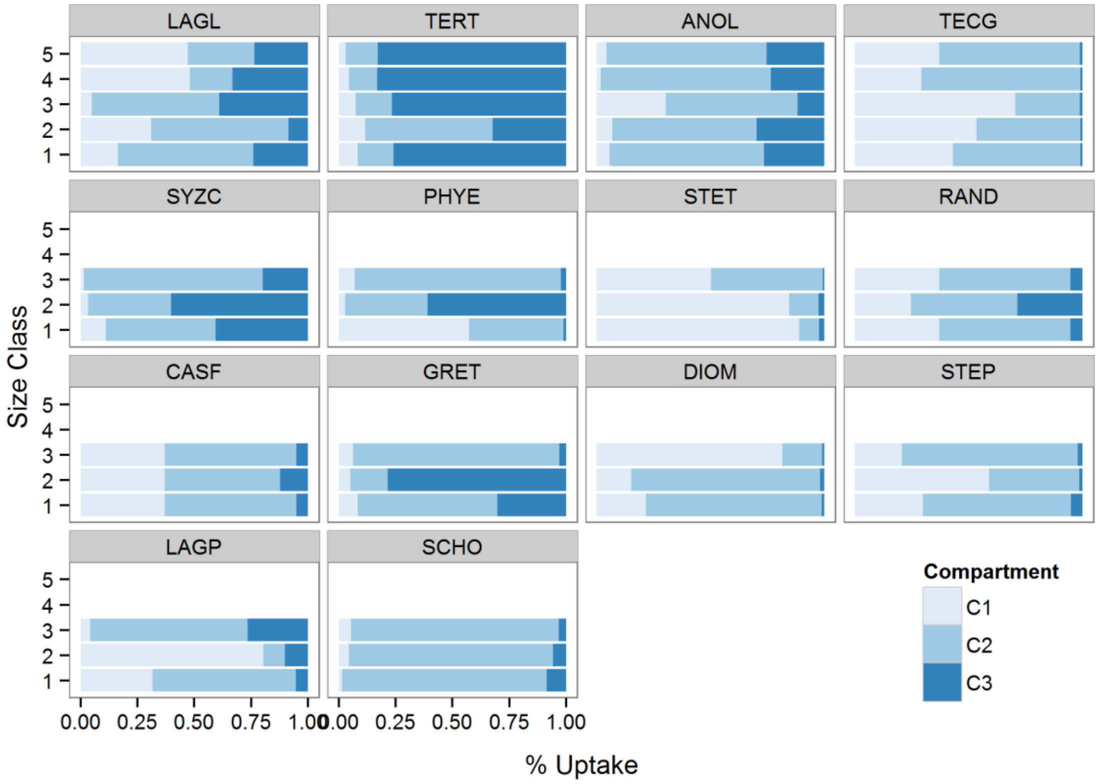


Supplementary Fig. 5b



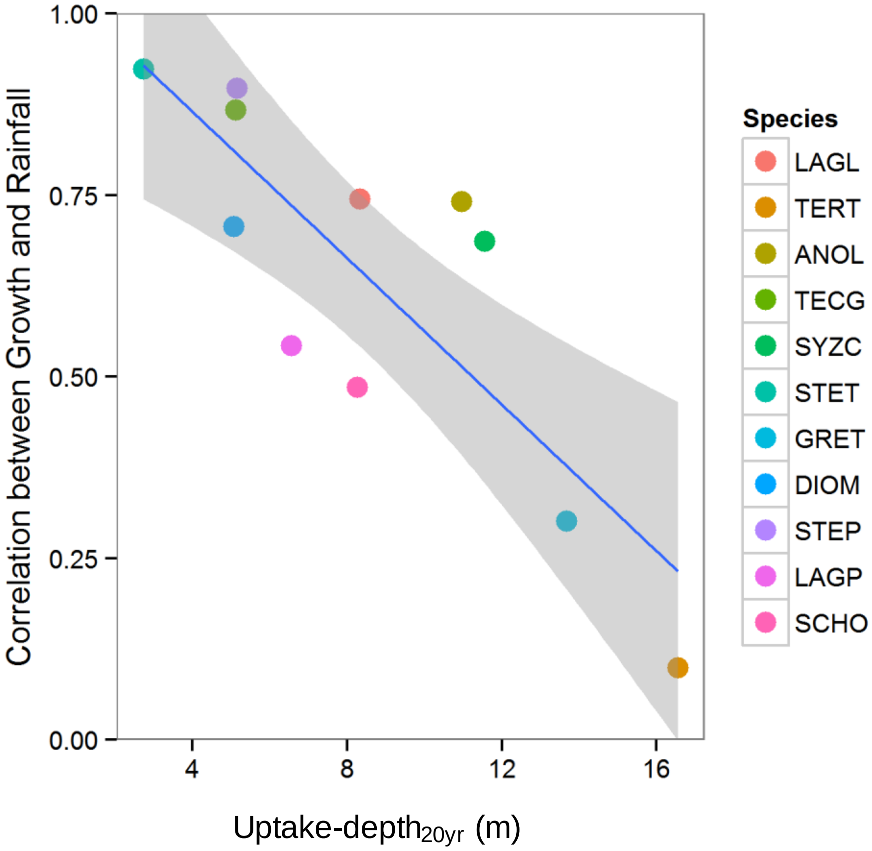
Supplementary Fig. 5 | Results of null model tests for mean community niche overlap for Uptake-Depth$_{20yr}$ and niche overlap with nearest neighbour. a, Observed mean community niche overlap index (red line, d-statistic; n = 91 species pairs, P < 0.001) is shown against null distribution generated with 10000 pseudo-communities by randomizing species niche breadth and using utilization matrix based on electivity. Dashed line indicates 5% bootstrapped quantile for the simulated pseudo-communities. b, Mean niche overlap based on electivity against Rank of Nearest Neighbour in niche space (n = 13 species pairs at each rank, P < 0.05 for ranks greater than four) is shown for both observed (pink) and simulated pseudo-communities (blue). Gray envelope depicts 5% to 95% CI for the simulated pseudo-communities.

Supplementary Fig. 6



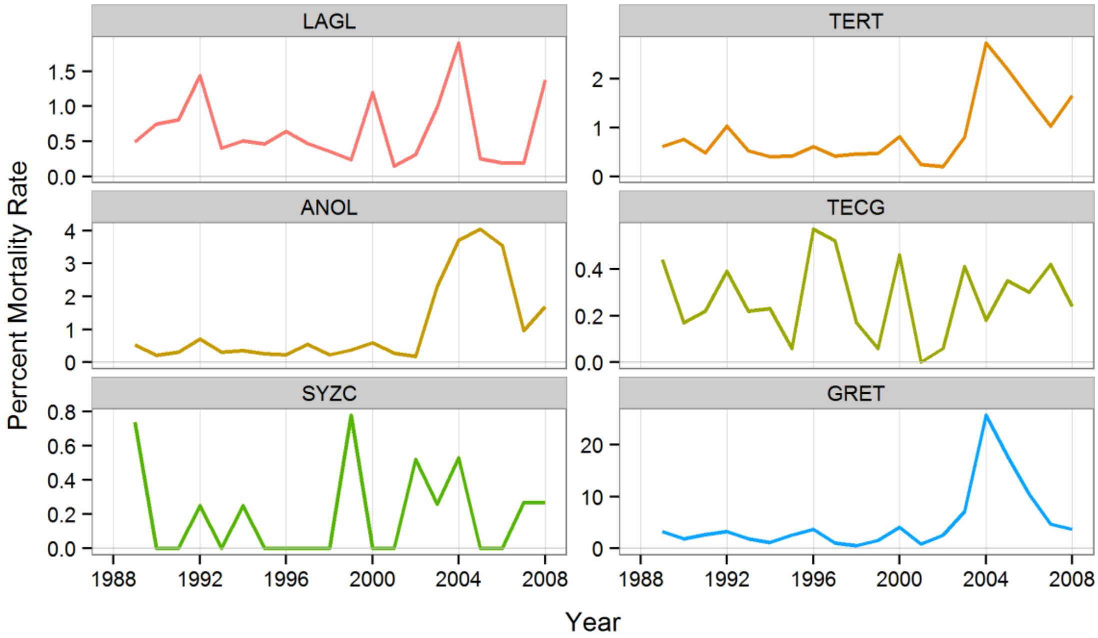
Supplementary Fig. 6 | Per cent water-uptake from each belowground compartment over 1992-2012 as estimated by the water-stress model for each species by size class. Size classes are based on equal quantiles within each species, with greater size class value corresponding to greater tree size. For each of the four co-dominant species five size classes are used, while three for rest of the species. See Supplementary Information for species codes (Supplementary Table 1).

Supplementary Fig. 7



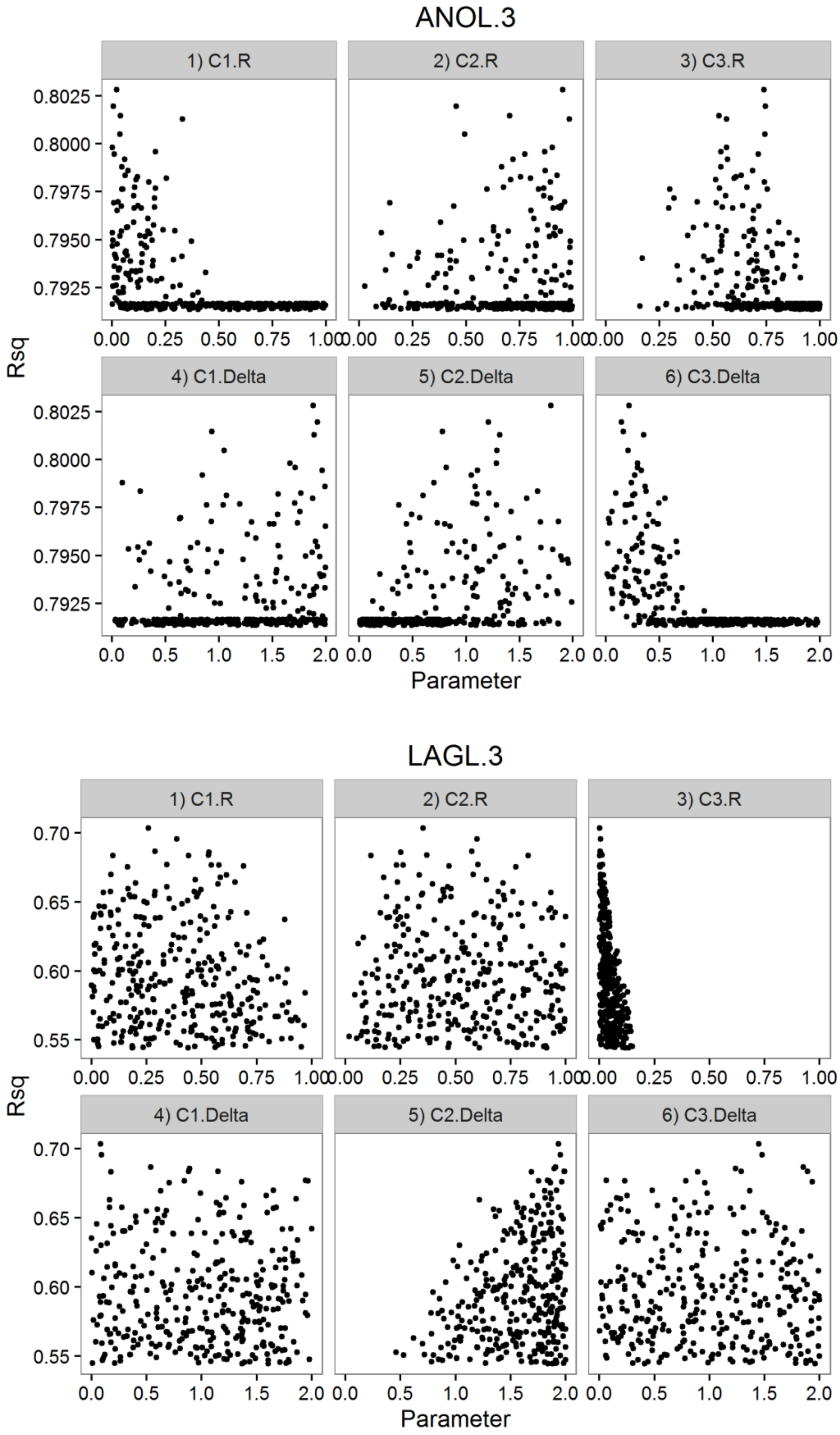
Supplementary Fig. 7 | Correlation between species growth rates and rainfall (at 4-year census intervals) as a function of species Uptake-Depth$_{20yr}$. Correlation (Pearson's product-moment correlation coefficient, r) between rainfall and observed growth rate for canopy species as a function of species Uptake-Depth$_{20yr}$ ($Corr_{Rainfall,Growth} = 1.06 - 0.047 \times$ Uptake-Depth$_{20yr}$; $n = 11$ species; $R^2 = 0.54$, $P = 0.004$). Grey envelope depicts point wise 95% confidence interval for the linear model. See Supplementary Information for species codes (Supplementary Table 1).

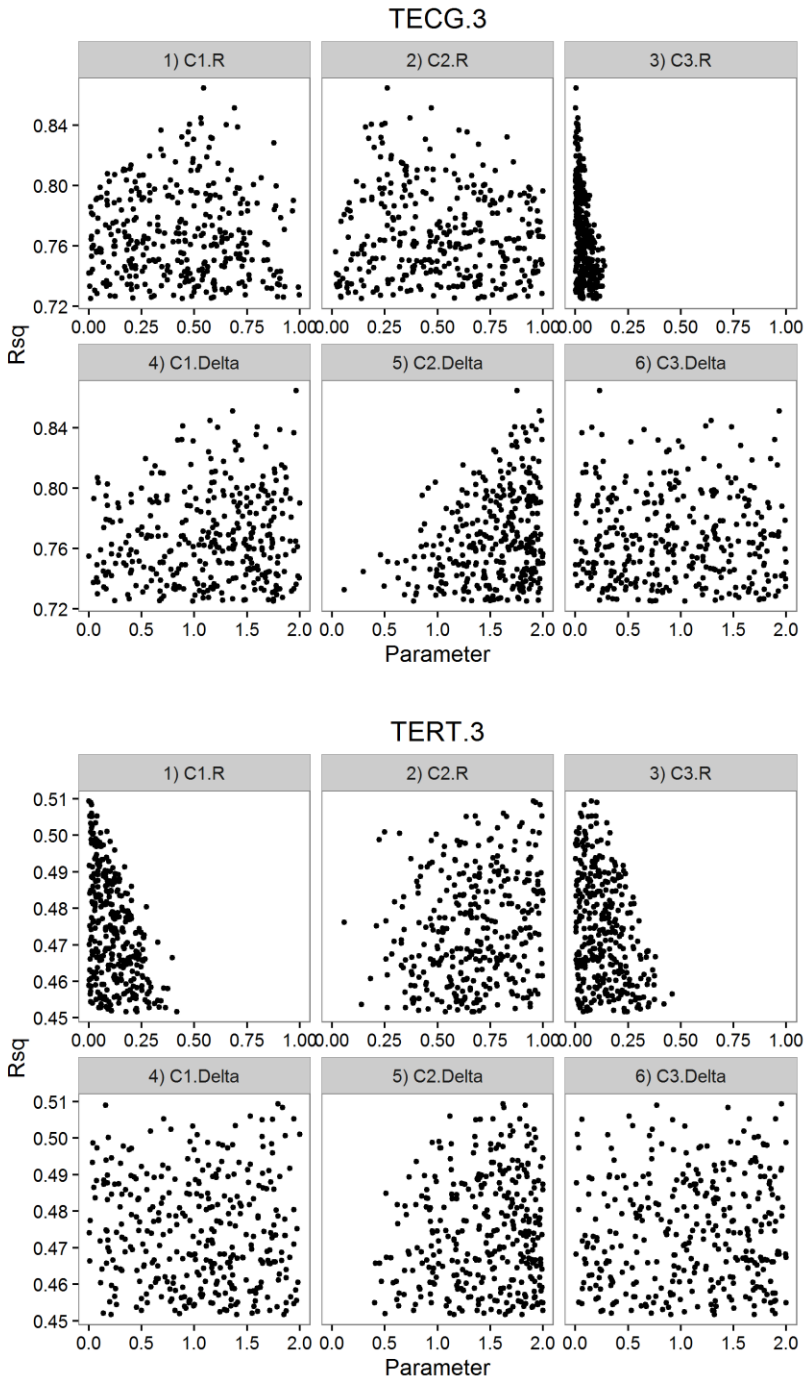
Supplementary Fig. 8



Supplementary Fig. 8 | Annual per cent mortality rates of tree species in the MFDP from 1089 to 2012. Data is shown for canopy species for which predrought (2003) abundance was greater than 300 trees. See Supplementary Information for species codes (Supplementary Table 1).

Supplementary Fig. 9





Supplementary Fig. 9 | Testing equifinality for the GLUE methodology used for the water-stress model: Scatter plots of R-sq versus parameter space (top 1500 that gave maximum R-sq) are shown for the six parameter: R and δ for each of the C1, C2 and C3 compartment for the four most common species: ANOL, LAGL, TECG and TERT for size class 3. Across all the species, parameters are well constrained i.e. issue of equifinality is absent at least for one parameter, but usually many. Thus best fitting parameters can be chosen.

Supplementary Information

Table 1. Species codes, species, genus, family, growth form and sample size (number of trees with complete growth records in Mudumalai MFDP) for the species for which effective rooting depth was calculated. Genus, Species and Family names are updated to reflect nomenclature in the Plant List (www.ThePlantList.org) as of August 11th, 2016.

S. N.	Species Code	Genus	Species	Family	Form	Sample Size
1	LAGL	*Lagerstroemia*	*microcarpa*	Lythraceae	canopy tree	2230
2	TERT	*Terminalia*	*crenulata*	Combretaceae	canopy tree	1867
3	ANOL	*Anogeissus*	*latifolia*	Combretaceae	canopy tree	1543
4	TECG	*Tectona*	*grandis*	Lamiaceae	canopy tree	1241
5	SYZC	*Syzygium*	*cumini*	Myrtaceae	canopy tree	291
6	PHYE	*Phyllanthus*	*emblica*	Phyllanthaceae	understorey tree	215
7	STET	*Stereospermum*	*tetragonum*	Bignoniaceae	canopy tree	188
8	RAND	*Catunaregam*	*spinosa*	Rubiaceae	understorey tree	117
9	CASF	*Cassia*	*fistula*	Leguminosae	understorey tree	113
10	GRET	*Grewia*	*tiliifolia*	Malvaceae	canopy tree	111
11	DIOM	*Diospyros*	*montana*	Ebenaceae	canopy tree	90
12	STEP	*Stereospermum*	*personatum*	Bignoniaceae	canopy tree	66
13	LAGP	*Lagerstroemia*	*parviflora*	Lythraceae	canopy tree	43
14	SCHO	*Schleichera*	*oleosa*	Sapindaceae	canopy tree	37

Table 2. Growth rate time series for species by size class in cm.yr^{-1}

Species Code	Size Class	Size Class (dbh cm)	Sample Size	1992-1996	1996-2000	2000-2004	2004-2008	2008-2012
ANOL	1	[6.7,15.9)	290	0.08	0.13	0.04	0.1	0.09
ANOL	2	[15.9,19.8)	305	0.09	0.16	0.06	0.14	0.12
ANOL	3	[19.8,23.7)	300	0.12	0.19	0.07	0.17	0.13
ANOL	4	[23.7,28.6)	301	0.14	0.23	0.08	0.19	0.16
ANOL	5	[28.6,41.8)	300	0.16	0.25	0.08	0.21	0.16
CASF	1	[1.5,7.9)	36	0.36	0.36	0.25	0.25	0.31
CASF	2	[7.9,10.5)	33	0.31	0.39	0.24	0.2	0.29
CASF	3	[10.5,19.6)	40	0.33	0.36	0.19	0.21	0.34
DIOM	1	[13.8,28)	28	0.15	0.29	0.27	0.43	0.16
DIOM	2	[28,35.3)	29	0.34	0.61	0.34	0.55	0.19
DIOM	3	[35.3,52.2)	30	0.43	0.69	0.4	0.67	0.24
GRET	1	[13.4,44.6)	33	0.33	0.48	0.22	0.36	0.36
GRET	2	[44.6,54)	37	0.41	0.64	0.29	0.34	0.46
GRET	3	[54,71)	37	0.54	0.74	0.51	0.51	0.39
LAGL	1	[2.6,17.3)	426	0.16	0.2	0.13	0.2	0.16

Table 2. Continued…

Species Code	Size Class	Size Class (dbh cm)	Sample Size	1992-1996	1996-2000	2000-2004	2004-2008	2008-2012
LAGL	2	[17.3,22.9)	436	0.28	0.31	0.21	0.34	0.28
LAGL	3	[22.9,28.6)	431	0.31	0.35	0.26	0.34	0.34
LAGL	4	[28.6,35.7)	429	0.42	0.46	0.33	0.45	0.42
LAGL	5	[35.7,52.9)	441	0.41	0.49	0.37	0.41	0.46
LAGP	1	[8.6,14.2)	13	0.12	0.15	0.01	0.13	0.11
LAGP	2	[14.2,17.5)	13	0.13	0.16	0.02	0.06	0.1
LAGP	3	[17.5,28.4)	15	0.03	0.18	0.01	0.1	0.18
PHYE	1	[9,17.6)	68	0.18	0.26	0.15	0.22	0.14
PHYE	2	[17.6,22.9)	69	0.13	0.2	0.12	0.17	0.17
PHYE	3	[22.9,35.7)	71	0.11	0.21	0.14	0.18	0.18
RAND	1	[4.8,25.9)	37	0.22	0.3	0.13	0.15	0.17
RAND	2	[25.9,32.1)	37	0.26	0.3	0.1	0.23	0.19
RAND	3	[32.1,46.7)	39	0.31	0.34	0.13	0.15	0.19
SCHO	1	[25.7,56.5)	11	0.16	0.37	0.18	0.27	0.19
SCHO	2	[56.5,69.9)	12	0.22	0.46	0.27	0.38	0.28
SCHO	3	[69.9,92.7)	12	0.06	0.42	0.18	0.26	0.14
STEP	1	[4.9,30.4)	21	0.27	0.39	0.15	0.38	0.25
LAGL	4	[28.6,35.7)	429	0.42	0.46	0.33	0.45	0.42
LAGL	5	[35.7,52.9)	441	0.41	0.49	0.37	0.41	0.46
LAGP	1	[8.6,14.2)	13	0.12	0.15	0.01	0.13	0.11
LAGP	2	[14.2,17.5)	13	0.13	0.16	0.02	0.06	0.1
LAGP	3	[17.5,28.4)	15	0.03	0.18	0.01	0.1	0.18
PHYE	1	[9,17.6)	68	0.18	0.26	0.15	0.22	0.14
PHYE	2	[17.6,22.9)	69	0.13	0.2	0.12	0.17	0.17
PHYE	3	[22.9,35.7)	71	0.11	0.21	0.14	0.18	0.18
RAND	1	[4.8,25.9)	37	0.22	0.3	0.13	0.15	0.17
RAND	2	[25.9,32.1)	37	0.26	0.3	0.1	0.23	0.19
RAND	3	[32.1,46.7)	39	0.31	0.34	0.13	0.15	0.19
SCHO	1	[25.7,56.5)	11	0.16	0.37	0.18	0.27	0.19
SCHO	2	[56.5,69.9)	12	0.22	0.46	0.27	0.38	0.28
SCHO	3	[69.9,92.7)	12	0.06	0.42	0.18	0.26	0.14
STEP	1	[4.9,30.4)	21	0.27	0.39	0.15	0.38	0.25
STEP	2	[30.4,43.4)	21	0.14	0.3	0.12	0.35	0.13
STEP	3	[43.4,72.3)	22	0.18	0.35	0.14	0.41	0.15
STET	1	[8.4,19.1)	58	0.14	0.18	0.13	0.27	0.14
STET	2	[19.1,25.3)	62	0.14	0.18	0.08	0.25	0.17
STET	3	[25.3,41.1)	62	0.07	0.18	0.11	0.22	0.1
SYZC	1	[13.1,27.7)	91	0.22	0.42	0.23	0.46	0.41
SYZC	2	[27.7,37.9)	94	0.36	0.58	0.24	0.52	0.52
SYZC	3	[37.9,60)	97	0.37	0.74	0.25	0.55	0.46
TECG	1	[10.1,33.1)	234	0.12	0.2	0.15	0.43	0.14
TECG	2	[33.1,40.7)	245	0.14	0.25	0.19	0.46	0.16

Table 2. Continued…

Species Code	Size Class	Size Class (dbh cm)	Sample Size	1992-1996	1996-2000	2000-2004	2004-2008	2008-2012
TECG	3	[40.7,48.1)	239	0.14	0.24	0.16	0.41	0.16
TECG	4	[48.1,57.3)	239	0.14	0.29	0.16	0.4	0.16
TECG	5	[57.3,77.4)	245	0.14	0.32	0.18	0.42	0.15
TERT	1	[8,17.4)	361	0.07	0.1	0.05	0.08	0.15
TERT	2	[17.4,23.6)	356	0.11	0.16	0.07	0.12	0.18
TERT	3	[23.6,31.7)	368	0.11	0.16	0.07	0.12	0.21
TERT	4	[31.7,42.8)	362	0.05	0.13	0.07	0.09	0.18
TERT	5	[42.8,65.9)	363	0.02	0.15	0.07	0.09	0.16

Table 3. Yearly abundances (>=1 cm DBH) of species for which ERD is calculated.

Year	ANOL	CASF	DIOM	GRET	LAGL	PHYE	RAND	SCHO	STEP	STET	SYZC	TECG	TERT
1988	2279	495	130	514	3652	561	626	73	99	330	407	1814	2770
1989	2265	459	126	493	3622	548	613	73	99	323	402	1803	2751
1990	2260	451	123	481	3583	534	593	73	98	320	401	1796	2729
1991	2251	430	121	462	3547	513	581	72	99	318	400	1785	2710
1992	2231	559	117	441	3521	493	575	70	96	318	393	1779	2677
1993	2224	549	117	431	3506	488	568	69	96	317	393	1774	2662
1994	2210	520	116	425	3461	474	546	69	91	316	394	1765	2647
1995	2204	494	116	411	3425	469	524	69	91	311	391	1765	2632
1996	2185	591	114	387	3378	452	497	71	94	306	387	1747	2603
1997	2173	561	114	381	3355	437	472	71	93	303	387	1737	2589
1998	2168	531	114	377	3341	427	463	70	93	300	387	1731	2574
1999	2160	519	114	371	3333	418	456	70	92	297	384	1729	2561
2000	2145	636	114	354	3282	397	444	69	92	291	386	1706	2535
2001	2137	620	114	351	3277	388	440	68	92	290	386	1705	2530
2002	2128	572	114	335	3240	370	419	68	91	288	381	1702	2515
2003	2078	536	112	311	3205	347	390	68	90	283	379	1694	2493
2004	2003	671	110	231	3189	312	364	67	92	280	376	1694	2423
2005	1921	602	110	191	3178	301	361	67	90	274	376	1690	2369
2006	1853	525	110	170	3184	297	341	67	90	270	376	1683	2330
2007	1835	457	110	162	3177	294	340	67	90	267	375	1676	2306
2008	1809	628	109	161	3259	289	302	67	93	271	373	1669	2276

Table 4. Yearly tree mortalities of species for which ERD is calculated.

Year	ANOL	CASF	DIOM	GRET	LAGL	PHYE	RAND	SCHO	STEP	STET	SYZC	TECG	TERT
1989	12	10	4	17	18	11	11	0	0	6	3	8	17
1990	5	7	1	9	27	14	10	0	0	3	0	3	21
1991	7	3	2	13	29	20	11	1	0	3	0	4	13
1992	16	10	2	15	51	18	13	0	0	2	1	7	28
1993	7	11	0	8	14	3	6	1	0	1	0	4	14
1994	8	14	0	5	18	8	10	0	0	1	1	4	11
1995	6	20	0	11	16	4	6	0	0	4	0	1	11
1996	5	4	1	15	22	9	12	0	0	4	0	10	16
1997	12	28	0	4	16	13	10	0	1	2	0	9	11
1998	5	30	0	2	12	10	4	1	0	3	0	3	12
1999	8	18	0	6	8	7	6	0	0	1	3	1	12
2000	13	19	0	15	40	22	12	1	0	3	0	8	21
2001	6	16	0	3	5	8	5	1	0	2	0	0	6
2002	4	17	0	9	10	14	8	0	0	1	2	1	5
2003	49	26	2	24	32	22	20	0	0	3	1	7	20
2004	77	48	1	80	61	37	32	0	1	8	2	3	68
2005	81	79	1	41	8	11	5	0	2	5	0	6	53
2006	68	70	0	20	6	4	16	0	0	4	0	5	38
2007	18	63	0	8	6	3	5	0	0	2	1	7	24
2008	31	60	1	6	44	6	25	1	0	2	1	4	38

Chapter 7

Summary and Future Directions

Summary and Future Directions

This thesis improved our understanding of plant ecology in several ways, locally, for the seasonally dry tropical forests in southern India, as well as in general, in terms of principles and novel methods that would be applicable for forests elsewhere.

Part I of Chapter 3 illustrated the remarkable extent of seasonal shrinkage and swelling in stem diameters and highlighted the problem of bias in woody growth estimates due to water-induced fluctuations. It also showed that dendrometers may not accurately capture diurnal variation in tree stem diameters – it likely underestimates the shrinkage, but that dendrometers can largely capture the extent of seasonal stem shrinkage and swelling.

By independently measuring woody growth for a sample of trees Part II of Chapter 3 presented a novel method to correct the hydrostatic bias at a 50-ha plot tree community level. This was done for 20-year long stem diameter time series measured using graduated tapes at 4-year scale. This chapter showed that although one expects that hydrostatic bias may not matter at long time scales of 4-years, in this forest woody growth is slow and difference in water-status of trees across successive censuses relatively large such that diameter change based woody growth estimates may still suffer from large hydrostatic biases. Here, bias should not be overlooked merely due to large number of years in between any two censuses—be it 4 years or 8 years; but the extent of bias really depends on difference in water-status of the tree at the time of those censuses. The extent of bias needs to be evaluated and corrected. This work also suggested that the temporal trend in mean community growth substantially changed after bias correction, and that one would likely obtain an erroneous relationship of growth with water availability without such a correction. This work calls for application of this method in permanent forest plots (PSPs) elsewhere, and reanalysis of temporal growth-climate, or growth-resource relationships. The extent of bias was found to differ across size classes. Although it was not found to be varying much across species, sample sizes and the diversity of species analysed were rather small. This needs to be investigated in future. The prospects for this were limited so far by the absence of reliable tree-ring based growth time series largely due to indistinguishable nature of tree-rings in tropical tree species, but new developments in techniques such as dendro-chemistry may open up possibilities. In the absence of more information on species-specific differences in the extent of hydrostatic bias and lack of appropriate corrective measure, no attempt was made in correcting species-specific time series of growth (Chapter 5).

In chapter 4 observations of seasonal fluctuations in tree stem diameters were presented for several seasonally dry tropical forest types PSPs along a rainfall gradient. Here drier forests showed stem shrinkages through the dry season, but these were largely absent for the wetter forests. The novel method of hydrostatic bias correction developed in Chapter 3 part II was applied here for 3-year long annual dendrometer-based stem diameter time series for each of the forest plots. It revealed that in the absence of bias correction, year-to-year variation in growth in dry forests was primarily due to large hydrostatic bias, and this led to highly misleading spatial forest growth-rainfall relationship for each year. After bias correction these relationships were rather stable across years. This highlighted the sensitivity of any "space for time" substitution modeling to the choice of the year, and the necessity of bias correction. Gradient analysis using 3-yr mean growth did not reveal a positive trend in growth-rainfall relationship; however, a marginal, but significantly positive trend was revealed after bias correction. Here it was also revealed that the way growth is dependent on size varies from dry to moist forests along the rainfall gradient, owing to the finding of a distinct allometry in the dry forest—also termed as a woodland savanna. This also meant that the growth-rainfall relationship along the spatial rainfall gradient was dependent on size. Overall this work calls for careful consideration of possible confounding factors in spatial rainfall gradient analyses in general.

The work in Chapter 5 makes a series of contributions. It breaks through the shortcoming of having to evaluate plant performance against rainfall as a proxy for plant water availability, and presents a way to estimate the variation in available water that trees actually respond to. The hydrological model demonstrates the heterogeneity in rhythms and dynamics of available water at different vertical depths—that this can generate ample opportunities for species to partition belowground water niches is hard to miss, each specialising on the dynamics of water at a particular depth, with differential responses to drought. The inverse way of modeling trees dynamic water uptake depth from their observed above-ground growth patterns provides a novel way of estimating this enigmatic variable. In the SDTF study site, it was found that species indeed diverged in their uptake depths. The approach reveals the way species partition the water resource by having differential water uptake depths, responding to the peculiar dynamics of water at the respective depths. Using uptake-depth measured thus, species mortality was found to be increasing with their water uptake depth under an extreme drought that emptied the deep vadose zone. This observation brings to light the untested nature of the common assumption that deep rooted trees are buffered against drought. This emphasised the importance of evaluating trees realized, not hypothesised drought. The general hypothesis that trees with deep water uptake are buffered in a drought may apply to short-term droughts. However, it just so happens that in this seasonally dry forest trees do not significantly die from water-stress when droughts are short, which might be a general adaptation to the regular seasonal droughts. Unlike shallow zones, drought in the deep vadose zone may have a long return frequency, which might get modified in future under global climate change. The observed uptake depth-dependent drought-induced mortality patterns combined with the model's finding for deep uptake species – highly suppressed growth under extreme drought, but steady growth otherwise – versus that for shallow-uptake species – low variation in woody growth in the presence or absence of drought – brings forth a new underlying demographic trade-off depending on water-uptake strategies.

This study on adult trees changes our understanding of how niche partitioning operates for these long lived organisms. The new eco-hydrological framework proposed here should enable us to analyze mechanisms and consequences of hydrological niche separation in PSPs across the globe, using existing long-term datasets on growth and mortality. This will advance our understanding of species coexistence in general. How water-uptake strategies are coordinated with other plant functional traits need to be further investigated. Although the exact spatial and temporal scales at which water varies may vary across different climatic and substrate conditions, there is no reason why the patterns and processes observed here leading to hydrological niche segregation and demographic trade-offs should not be widespread. The signal dampening of water by depth is observed commonly. Although it is reported more from agricultural sites (Entin et al., 2000; Turkeltaub et al., 2014), in forested catchments where uptake can be far deep, differences in dynamics by depth is expected to be even greater. Whether deep water-uptake species are vulnerable to extreme drought globally needs to be investigated and the climate consequences of such a scenario need be evaluated.

To move towards a global synthesis on how hydrology drives forest demography, especially in droughts, and how hydrological niches are partitioned, a possible flow is presented below. It includes for the skeptics an alternative testing of the specific part of the eco-hydrology framework that infers species water-uptake depths. It should be, however, noted that rooting depths are not equivalent to water-uptake depths, and would not add too much corroborative evidence. The methods of estimating water-uptake depth by natural isotopic gradients are limited to top 1 or 2 meters and may not be suitable for the study system, where water uptake may be taking place from 5 to 15 m deep. Artificial tracer experiments may achieve these depths, but this method would be very demanding and may need to be carried out over several years, before sufficient evidence could gather, for else they may reveal only transient relative or absolute uptake depths that may be even contradictory to model predictions.

The flowchart thus moves onto testing the generality of how belowground water availability shapes distinct species specific drought responses across diverse forests in terms of growth and mortality and hydrological niche partitioning.

1. **Test the empirical support** for estimates of species uptake-depths that are inversely inferred from growth responses to belowground water availability by adapting some comparable independent method—with the awareness that they may prove inadequate, especially at the depths and scales involved.
2. Review across diverse forested catchments the **generality of differential dynamics of water by depth** as a mechanism generating numerous belowground niches for tree species. This is expected and shown in agricultural sites, but not in forested catchments where uptake can be far deep and differences in dynamics by depth even greater. Test if across sites relative water availability in shallow vs. deep vadose zone is inversed in short vs prolonged droughts-- potentially giving rise to differential drought responses?
3. **Apply the eco-hydrology framework in diverse forested sites** and test whether species growth responses are driven by differential actual belowground water availability at depths that they are tuned to—using the inverse modeling framework. Use this to test how hydrological niches are partitioned.
4. Identify from the actual belowground water availability in the observed droughts whether shallow or deep water-uptake trees are expected to die more: deep-uptake ones in prolonged droughts, shallow-uptake ones in short droughts. Do species mortality patterns in the given droughts match well with their identified water-uptake depths from the inverse model?

References

Entin, J.K., Robock, A., Vinnikov, K.Y., Hollinger, S.E., Liu, S., Namkhai, A., 2000. Temporal and spatial scales of observed soil moisture variations in the extratropics. J. Geophys. Res. Atmospheres 105, 11865–11877. doi:10.1029/2000JD900051

Turkeltaub, T., Dahan, O., Kurtzman, D., 2014. Investigation of groundwater recharge under agricultural fields using transient deep vadose zone data. Vadose Zone J. 13.

Affiliation of Co-Authors

Prof. Raman Sukumar

Centre for Ecological Sciences and
Divecha Centre for Climate Change
Indian Institute of Science
Bangalore 560012, India

Dr. Laurent Ruiz

INRA, Agrocampus Ouest, UMR1069
Sol Agro et hydrosystème Spatialisation
Rennes 35000, France
&
Indo-French Cell for Water Sciences
IISc-IRD Joint Laboratory
Indian Institute of Science
Bangalore 560012, India

Mr. H. S. Dattaraja

Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560012, India

Mr. H. S. Suresh

Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560012, India

Dr. Jean Riotte

IRD, UMR 5563 GET
Université de Toulouse
CNRS, 31400 Toulouse, France
&
Indo-French Cell for Water Sciences
IISc-IRD Joint Laboratory
Indian Institute of Science
Bangalore 560012, India

Prof. M.S.M. Kumar

Dept. of Civil Engineering and
Indo-French Cell for Water Sciences
IISc-IRD Joint Laboratory
Indian Institute of Science
Bangalore 560012, India

Dr. Sean M. McMahon

Smithsonian Institution Global Earth Observatory
Smithsonian Environmental Research Center
Edgewater, MD 21037, USA

Mr. Sandeep Pulla

Centre for Ecological Sciences
Indian Institute of Science
Bangalore 560012, India