# Growth, hydraulics and functional traits of *Melia dubia* across a steep climatic gradient in southern India

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# DEDICATION

I dedicate this work to my mother the late Smt. Puttiramma, aunt late Smt. Gowramma, uncles late Sri. Kaliveerappa and late Sri. K.S. Nagaraju and all the members of *Erappa's* family, for cherishing the value of education in their hearts and encouraging individuals.

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# Summary

The global demand for wood has been continuously increasing and the world is also witnessing large-scale deforestation. This is largely contributing to global warming, land degradation and biodiversity loss. Quite a large number of countries in the world are importing wood and wood products for meeting domestic demands. In India, for example, the import value of wood and wood products increased from 0.04 billion USD in 1961 to 8.7 billion USD in 2019. Existing forest policy regimes and economic reforms are expected to create additional demand for wood and shortage of domestic supply in the future. To reduce the pressure on forests and to ensure wood supply, short rotation plantations with native and exotic tree species are being promoted in agroforestry and farm forestry systems. For augmentation of domestic wood production and to fetch early income to the farmers, *Melia dubia* Cav. (Meliaceae) has been identified as one of the potential Indian native species for plantations and agroforestry systems. To explore the ecology and production potential of the species an investigation was set up with following the objectives: (1) determination of factors controlling tree growth across a rainfall gradient and (2) exploration of variation in growth-determining hydraulic wood and leaf traits in *M. dubia*.

In a first regional-scale study, we studied 186 *M. dubia* farmland woodlots, aged between one and nine years and covering a rainfall gradient from 420 to 2170 mm yr$^{-1}$ located in the South Indian states of Andhra Pradesh, Karnataka and Tamil Nadu. All studied *M. dubia* woodlots were established on former agricultural land. To avoid early-stage failures of the woodlots, all interviewed farmers irrigated the seedlings for at least one growing season. Most farmers (66%) continued supplemental irrigation for more than one growing season, but with reduced irrigation frequencies. A total of 34% moved to exclusively rainfed cultivation after the initial irrigation period; the mean annual precipitation at all non-irrigated woodlots was higher than 670 mm yr$^{-1}$. The computed power-law growth model predicts an average stand-level aboveground biomass of 93.8 Mg ha$^{-1}$ for nine-year-old woodlots. The resulting average annual aboveground biomass increment over the length of the rotation cycle is 10.4 Mg ha$^{-1}$ yr$^{-1}$, which falls within the range reported aboveground biomass increment for other tropical

tree plantations. The parameters of the growth model expressed as functions of management, climate and soil variables, explain 65% of the variance in aboveground biomass. The results indicate that water availability is the main driver of the growth of *M. dubia*. Compared to the effects of water availability, the effects of soil nutrients are 26% to 60% smaller. We conclude that because of its high biomass accumulation rates in farm forestry, *M. dubia* is a promising candidate for short-rotation plantations in South India and beyond.

The second study investigated the intra-specific variability in growth performance, leaf traits, and wood anatomical and derived hydraulic properties in 31 *M. dubia* plantations along a steep rainfall gradient from 450 to 1700 mm yr$^{-1}$, and addressed the role of different irrigation practices and soil nutrient availability. We found water supply and soil nutrient status to have a dominant influence on the aboveground biomass increment of *M. dubia*. aboveground biomass increment was higher at irrigated sites with a less negative climatological water balance (i.e. with lower rainfall) and sites with higher soil phosphorus availability. Stem wood anatomical traits associated with the water transport capacity mirrored the patterns in aboveground biomass increment. At sites with higher water and soil phosphorus availability, the xylem was composed of larger vessel diameters and lower vessel densities. However, both branch wood anatomical traits and leaf traits including the leaf-to-sapwood area ratio were largely independent of water availability and soil conditions.

In conclusion, our study underscores that water availability is the main driver that controls the growth of *M. dubia* and that the effects of soil nutrients comparatively smaller. Further, the detected larger xylem vessel diameters and lower vessel densities and resultant high stem hydraulic efficiency, at sites with higher water and soil phosphorus availability highlights prerequisites for high aboveground productivity and growth. The results also indicate that the short-rotation plantations of *M. dubia* will clearly benefits from continuous irrigation in regions that receive annual precipitations substantially below 1000 mm yr$^{-1}$. This also highlights the potential to increase yields in this important short-rotation forest species by improving irrigation and fertilization protocols.

# Zusammenfassung

Die weltweite Nachfrage nach Holz steigt kontinuierlich während die globale Waldfläche weiter schrumpft. Dies trägt in hohem Maße zur globalen Erwärmung, Landverödung und zum Verlust der biologischen Vielfalt bei. Viele Länder importieren Holz und Holzprodukte, um den heimischen Bedarf zu decken. In Indien stieg der Importwert von Holz und Holzprodukten beispielsweise von 0,04 Mrd. USD im Jahr 1961 auf 8,7 Mrd. USD im Jahr 2019. Es wird erwartet, dass durch forstpolitische Maßnahmen und Wirtschaftsreformen eine zusätzliche Nachfrage nach Holz bei gleichzeitiger Verknappung des inländischen Angebots entsteht. Um die verbleibenden Waldökosysteme zu entlasten und die Holzversorgung sicherzustellen, werden in Agroforst- und Farmforstsystemen verstärkt Kurzumtriebsplantagen mit einheimischen und exotischen Baumarten gefördert. Die Baumart *Melia dubia* Cav. (Meliaceae) wurde als eine vielversprechende einheimische Art Indiens für Plantagen und Agroforstsysteme identifiziert. Um das Produktionspotenzial von *M. dubia* genauer zu untersuchen, wurde in der vorliegenden Arbeit eine Untersuchung mit folgenden Zielen durchgeführt: (1) Bestimmung von Faktoren, die das Baumwachstum über breite Niederschlagsgradienten hinweg steuern, und (2) Untersuchung von Variationen in wachstumsbestimmenden hydraulischen Holz- und Blattmerkmalen von *M. dubia* .

In einer ersten Studie auf regionaler Ebene untersuchte wir 186 *M. dubia* Farmforstsysteme im Alter zwischen einem und neun Jahren und mit einem Niederschlagsgradienten von 420 bis 2170 mm pro Jahr in den südindischen Bundesstaaten Andhra Pradesh, Karnataka und Tamil Nadu. Alle untersuchten *M. dubia* Kurzumtriebsplantagen wurden auf ehemaligen landwirtschaftlichen Flächen angelegt. Um frühzeitige Ausfälle der Flächen zu vermeiden, bewässerten alle befragten Landwirte die Bäume mindestens eine Vegetationsperiode lang. Die meisten Landwirte (66%) setzten die Bewässerung für mehr als eine Vegetationsperiode fort, jedoch mit reduzierten Bewässerungshäufigkeiten. Insgesamt 34% der Landwirte stellten die anfängliche Bewässerung nach und nach ein. Der mittlere jährliche Niederschlag auf diesen unbewässerten Flächen war höher als 670 mm Jahr$^{-1}$. Das angewandte Wachstumsmodell prognostiziert eine durchschnittliche oberirdische Bestandesbiomasse von 93,8 Mg ha$^{-1}$ für neun Jahre alte *M. dubia* Plantagen. Der resultierende durchschnittliche jährliche Biomassezuwachs über die Dauer des Rotationszyklus beträgt 10,4 Mg $ha^{-1}$ $Jahr^{-1}$, was in den Bereich fällt, der für viele andere tropische Baumplantagen typisch ist. Die Parameter des Wachstumsmodells, ausgedrückt als Funktionen von Bewirtschaftungs-, Klima- und Bodenvariablen, erklären 65% der Varianz in der oberirdischen Biomasse. Die Ergebnisse zeigen, dass die Verfügbarkeit von Wasser der hauptsächliche limitierende Faktor für das Wachstum von M. dubia ist. Im Vergleich zu den Auswirkungen der Wasserverfügbarkeit sind die Auswirkungen von Bodennährstoffen um 26% bis 60% geringer. Wir schlussfolgern, dass *M. dubia* aufgrund seiner hohen Wachstumsraten ein vielversprechender Kandidat für Kurzumtriebsplantagen in Südindien und darüber hinaus ist.

Die zweite Studie untersuchte die intraspezifische Variabilität in der Wachstumsleistung, den Blattmerkmalen und anatomischen und abgeleiteten hydraulischen Holzeigenschaften in 31 der 186 *M. dubia* Plantagen, entlang eines steilen Niederschlagsgradienten von 450 bis 1.700 mm pro Jahr und mit unterschiedlichen Bewässerungspraktiken und Nährstoffverfügbarkeiten. Wir fanden heraus, dass die Wasserversorgung und der Nährstoffstatus des Bodens einen dominanten Einfluss auf das oberirdische Biomassewachstum von *M. dubia* haben. Der jährliche Biomassezuwachs erreichte in bewässerten Plantagen mit einer weniger negativen klimatologischen Wasserbilanz (d. h. mit höheren Niederschlägen) und an Standorten mit höherer Phosphorverfügbarkeit im Boden hohe Werte. Die anatomischen Merkmale des Stammholzes, die mit der Wassertransportkapazität verbunden sind, spiegelten die Muster im Jährliche Biomassezuwachs wider. An Standorten mit höherer Verfügbarkeit von Wasser und Phosphor im Boden hatte das Xylem größere Gefäßdurchmesser bei geringeren Gefäßdichten. Hingegen waren sowohl die anatomischen Merkmale des Astholzes als auch die erfassten Blattmerkmale weitgehend unbeeinflußt von der Wasserverfügbarkeit und den Bodenbedingungen.

Zusammenfassend unterstreicht wir Studie, dass die Wasserverfügbarkeit der Haupttreiber für das Wachstum von *M. dubia* ist während der Einfluss von Bodennährstoffen vergleichsweise

geringer ist. Die beschriebenen größeren Xylemgefäßdurchmesser und geringeren Gefäßdichten an Standorten mit höherer Verfügbarkeit von Wasser und Bodenphosphor und die daraus resultierende hohe hydraulische Effizienz führen zu hohem oberirdischen Biomassewachstum. Kurzumtriebsplantagen mit *M. dubia* profitieren eindeutig von kontinuierlicher Bewässerung, vor allem in Regionen mit jährlichen Niederschlägen unter 1.000 mm. Dies unterstreicht auch das Potenzial zur weiteren Ertragssteigerung in *M. dubia* Plantagen durch optimierte Bewässerungs- und Düngestrategien.

# Chapter 1: General introduction

## 1.1. Study background

### *1.1.1. Forest resources and wood demand in India*

India, a country hosting ~ 18% of the world population on 2.3% of land area has 71.37 million ha land surface under forest (FAO and UNEP, 2020; FSI, 2021), imports 8.72 billion US$ worth of wood and wood products in 2019 (FAO, 2021). Even though it is 10th most forested country in the World (FAO and UNEP, 2020), but still it is striving to bring 33% of its geographical area under forest cover with proper policy initiatives and by professing an ecosystem approach to reach Sustainable Development Goal (SDG,15.1.1) (FAO and UNEP, 2020) and Bonn Challenge with commitment for restoration of 26 million ha degraded land by 2030 (Bonn Challenge, 2017). Nonetheless, existing forests in the country are subjected to different degrees of deforestation and degradation due to economic, anthropogenic and developmental pressure (Tian et al., 2010; Roy et al., 2015; Reddy et al., 2016). Population growth, poverty and agricultural expansion have been identified as prime driving forces of deforestation (Roy et al., 2015; Tollefson 2015; Reddy et al., 2016). Thus, increasing tree cover on agricultural lands is being identified as a practical solution and an available option (Ghosh and Sinha, 2018). Further, it was reported that the land greening process in India is mostly occurring on croplands (82%) whereas the contribution from forests (4.4%) was meagre (Chen et al., 2019).

The accounted annual wood production from agroforestry, farm forestry and trees grown outside forests in the country was 42 million cubic meters (FSI, 2011) which was about 13 times higher than timber production from forest and forest development corporations (Shrivastava and Saxena, 2017). However, the reduced wood supply from the forest and increased demands for wood and wood products resulted in increased imports (Chauhan and Chauhan, 2011; Shrivastava and Saxena, 2017; Ghosh and Sinha, 2018; FAO, 2021). This leads to the exploration of potential alternatives for augmenting domestic wood supply and protecting the existing forests (MoA, 2014; Ghosh and Sinha, 2019). Hence, the short rotation agroforestry has attained success with private initiatives and popular agroforestry species such as *Populus deltoides*, *Eucalyptus tereticornis*, *Casuarina equisetifolia*, *Acacia mangium*, *Ceiba pentandra*, *Toona ciliata*, *Gmelina arborea*, *Leucaena leucocephala*, *Melia dubia*, *Prosopis juliflora* in the country (Chauhan and Chauhan, 2011). Private companies are also promoting investment in long-term teak, sandalwood and red sanders plantations (Chauhan and Chauhan, 2011; Parthiban et al., 2021). However, India's import value of wood and wood products increased from 0.04 billion USD in 1961 to 8.7 billion USD in 2019 (FAO, 2021), which is in synchrony with the rising Gross Domestic Product growth (World Bank, 2021). Prevailing forest policy and economic reforms are expected to create additional demand for wood and a severe shortage of domestic supply in the future (Ghosh and Sinha, 2016; Shrivastava and Saxena, 2017).

### *1.1.2. Opinion on exotics and native species in wood production*

A growing number of studies have investigated the potential negative impacts of some commonly used exotic species on soil, water and biodiversity (Hughes, 1994; Zomer et al., 2007; Rangan et al., 2010; Joshi and Palanisami, 2011; Bilal et al., 2014; Zhou et al., 2020). This has led to a ban on *eucalyptus* and *acacia* plantations in some southern states of India (GOK, 2017). In light of the adverse effects of exotic species, native tree species are being encouraged in recent years (Amazonas et al., 2018; Liu et al., 2018; Castro-Díez et al., 2019; Zhou et al., 2020).

### *1.1.3. Emergence of Melia dubia*

For quick augmentation of domestic wood production and to fetch early income to the farmers, *M. dubia* has been identified as one of the potential native species for plantation and agroforestry to supply industrial wood (Chauhan and Chauhan, 2011; Parthiban et al., 2021). During 1990s the Hunsply, a plywood company in Karnataka initiated *M. dubia* plantations (Hunsply, 2022). Now, the state forest departments, academia and private enterprises promoting *M. dubia* as the main agroforestry and farm forestry tree species in the country. Despite this reported potential of the species to supply wood products, sufficient research has not yet been conducted to analyze the growth potential under different climatic regimes and management practices for assured economic returns.

### *1.1.4. Importance of aboveground biomass (AGB) estimation*

Agroforests are being considered as important carbon stocks (Zomer et al., 2016; Löf et al., 2019), however their accountability is not systematically assessed and counted in global and national carbon budgets (Zomer et al., 2016; Betemariyam et al., 2020). At the same time, an accurate estimate of *AGB* is required for implementation of REDD+ initiatives and for a better understanding of the carbon cycle (Campioli et al., 2016; Betemariyam et al., 2020). Identification of a reliable allometric model is needed for realizing benefits from carbon sequestration, or $CO_2$ emission reduction through the management of terrestrial woody biomass (Chave et al., 2014). However, no such species-specific biomass-estimation allometries are currently being available for *M. dubia* in the country and productivity quantification is also limited to the trees grown in experimental plots (Kirankumar and Patil, 2017; Thakur et al., 2018).

### *1.1.5. Research gaps and objectives*

In spite of the successful promotion of *M. dubia* in farm and agroforestry and its extensive distribution across hydroclimatic regimes, studies dealing with the growth and performance of trees across climatic and edaphic conditions and management regimes such as planting densities and irrigation were largely absent. Further, almost no attention was paid to research concerning photosynthesis and tree physiology. The water requirement of the tree and growth-linked hydraulics architecture of the species was not studied. Therefore, the following objectives were set for exploration in the study. (i) Quantification of aboveground biomass and growth rates of *M. dubia* and identify their controlling factors, with a focus on the role of natural and artificial water supply and their interaction. (ii) Effect of reduced water and nutrient availability on aboveground biomass increment and its consequential expression in xylem vessels and resultant hydraulic efficiency in similar-sized stems. Further, iii) resource-constrained expression in leaf traits such as leaf-to-sapwood area ratio (formation of smaller and thicker leaves) and iv) isotope signatures for more frequent stomatal closure, were explored.

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# Chapter 2: Literature review

## 2. Review of literature

Tree planting in forest land or on the agricultural landscapes is viewed as potential means for increasing terrestrial carbon sequestration and thereby reducing global warming and preventing land degradation and biodiversity loss (Bastin et al., 2019; Domke et al., 2020; Reppin et al., 2020; Girardin et al., 2021). Recent research advocates that natural secondary succession of native forest tree species is likely the preferred option from an ecological point of view (Lewis et al., 2019), however, agroforests, farm woodlots and tree plantations are land-use options that can balance ecological and socio-economic needs (Ghazoul et al., 2019; Guariguata et al., 2019; Dave et al., 2019). Deforestation is substantially contributing to global carbon emissions (Houghton and Nassikas, 2018). Sustainable production and consumption of forest products are essential to arresting deforestation, transforming agriculture and food systems (FAO, 2020). Therefore, complete information on tree species, exotic or native, is required for the farmers to make an informed decision about integrating trees into the farming enterprises. Hence, the species, *Melia dubia* has been studied for its biomass production potentials and its controls along with variability in growth-determining hydraulic wood and leaf traits across a steep water availability gradient in southern India. In this chapter, relevant literature is reviewed on controls of tree biomass production and growth determining anatomic and hydraulic traits.

### 2.1. *Melia dubia* Cav.

The genus *Melia*, belongs to the order Sapindales and family Meliaceae (Kubitzki, 2011). According to the fossil evidence, the genus *Melia* evolved in the region of Indochina during the Middle–Lower Miocene period (Muellner et al*.,* 2003, 2006 and 2009; Liao et al., 2016). The name, *Melia* is derived from the classical Greek name used by Theophrastus referring to the compound leaf pattern of the species *Fraxinus ornus* (Quattrocchi, 1999). Globally, *M. dubia* is found in Sri Lanka, Malaysia, Indonesia, the Philippines and Australia, (Nasayao et al*.*, 1994; Parthiban et al., 2009; Rambey et al*.*, 2019). Species was also introduced to South Africa, the Middle East, America (Bermuda, Brazil and Argentina), SE Asia–Pacific islands and Southern Europe (Sharma et al., 2019). *M. dubia* is naturally found in moist and dry deciduous forests of

India (Warrier, 2011, Thakur et al.,2020). According to the Plants of the World Online (POWO, 2022), *Melia azedarach* L. and *Melia dubia* Cav. are the two *Melia* species found in India. However, *M. composita* Wild. and *M. birmanica* Kurz. are treated as synonymous species under *M. dubia*. The natural distribution of *M. dubia* in South and south-eastern Asia indicates wider adaptability of species and literature records its introduction to the oldest tropical polyculture planting system (Rainforestation Farming) in the Philippines (Nguyen et al., 2016), energy plantations in Ghana (Wunder, et al., 2012) and for ex-situ conservation scheme in Sri Lanka (Munasinghe, 2004).

### ***2.1.1. Cultivation and its complementary traits***

The reviewed literature records the deployment of *M. dubia* in plantation forestry programs in south-eastern Asia in the late eighties (Nasayao et al., 1994). However, species gained greater attention during the first decade of this century as a main plantation and agroforestry tree in India (Thakur et al., 2018; Sinha et al., 2019; Thakur et al., 2020), due to the consequences of invasive exotics, increased attention has been paid towards natives (GOK, 2017) and also for fetching higher economic returns (Goswami et al., 2020). The complementary silviculture traits which make *M. dubia* attractive for cultivation are many. It is a deciduous tree (Warrier, 2011; Thakur et al., 2020) and reportedly grows up to 6 to 25 m in height with girth at breast height ranging from 1.2 to 1.8 m and a straight-bole up to 5-7 m (Sharma et al., 2019). Fast growth, straight and round bole, self-pruning, good coppicing, light-demanding and adaptability to a wide range of climatic and soil types have made *M. dubia* one of the most preferred tree species among planters (Nasayao et al., 1994; Parthiban et al., 2009; Sharma et al., 2012, 2017 and 2019). A Funnel-shaped canopy of compound leaves with bipinnate, rarely few tri-pinnate rachii, measuring 0.2 to 1.3 m long, forms foliaceous crown which facilitates light penetration to the understory crop (Thakur et al., 2018).

The wood produced is reportedly resistant to termite and fungi infestation (Suprapti, 2010) and is also preferred for plywood and engineered-wood industries (Parthiban et al., 2009; Thakur et al., 2018; Sinha et al., 2019; Thakur et al., 2020), furniture, agricultural tools and construction purposes (Mandang and Artistin, 2003). Further, its suitability for the paper and pulp industry has been explored (Saravanan 2013a; Sinha et al., 2019). The green foliage and fruits are good source of fodder for sheep and goats (Suresh 2013). Reported economics of tree cultivation over a hectare area fetches income of ₹ 8000 to ₹ 12000 (USD, 101 to 152) per month to the planters in a short rotation period of 10-12-year (Warrier, 2015; Sharma et al., 2017; Hunsply, 2022).

### *2.1.2. Reasons for its quick adoption in agroforestry and farm forestry system*

The media hype coupled with farmers' interest in earning early income in a short rotation period, is one of the main reasons for the quick adoption of the species. Large-scale nursery practices by private and public nurseries, ensured the availability of planting material. Assurance of end-to-end management service from private agencies linked with incentives and support (planting material and finance) from plywood and other wood-based industries (to comply with national forest policy directive of sourcing raw material supply from private forests) (Chinnaraj and Malimuthu, 2011; Saravanan et al., 2013a; Warrier, 2015). Promotion of *M. dubia* cultivation by state forest departments and research institutes (Warrier, 2015; Ramesha et al., 2018), followed by complementary awareness in the farming community about deforestation and its impact on rainfall, have been providing a needed fillip to the large-scale adoption. Further, changes in land resource allocation patterns owing to professional shift and labour-intensive agricultural crop production. Additionally, negative opinions and controversies surrounding the monoculture of exotics on soil health, water resources and ecological threats, push for the cultivation of native trees. Ban of planting of *Eucalyptus* and *Acacia* species (Joshi and Palanisami, 2011, GOK, 2017) and relatively long rotation of teak encouraged the emergence of *M. dubia* as a popular plantation and agroforestry tree species for the rainfed and irrigated condition in India. Government policies are also being amended to encourage *M. dubia* cultivation by relaxing the forest policy regulations concerning felling and transit of *M. dubia* trees cultivated over non-forest areas and on private lands in the states of Karnataka and Punjab (GOI, 2020). Further, it is expected that other states in the country may also follow the suit as many farmers are already cultivating *M. dubia* across Indian states.

### *2.1.3. Medicinal, aromatic and pesticidal use of M. dubia*

*M. dubia* contains many medicinal, aromatic and pesticidal important components such as alkaloids, carbohydrates, steroids, tannins, flavonoids, saponins, glycosides (Valentina et al., 2013), monoterpenes, sesquiterpene (Nagalakshmi et al., 2001; Saptha and Ramjaneyulu, 2007), toosendanin (Koul et al., 2002), salannin (de Silva et al., 1969), 2-chlorobenzimidazole (Jeyaleela et al., 2017) and many other chemical constituents (Tan et al., 2021). The presence of these components finds profound use of the species in medicinal, aromatic, biochemical and pesticide industries (Sivaraj et al., 2018). Further, substantial positive allelospoly of *M. dubia* on *Aloe vera* (Thakur et al., 2018) and *Cymbopogon flexuosus* (Thakur et al., 2020) was recorded. Such an effect on medicinal and aromatic plants enhances *M. dubia* adoption under agroforestry systems with specific planting geometries (Thankur et al., 2018 and 2020).

### *2.1.4. Wood quality and its industrial suitability*

The wood of *M. dubia* has a niche market in plywood industries (Sharma et al., 2017). Therefore, studies have been conducted to reveal the anatomy of wood (Saravanan et al., 2013b) physical and mechanical properties (Sharma et al., 2012; Saravanan et al., 2014), working qualities (Nazma et al., 1981; Ruwanpathirana 2014) fuel qualities (Saravanan et al., 2013c) and suitability to paper and pulp industries (Chinnaraj and Malimuthu 2011; Saravanan et al., 2013a; Sinha et al., 2019). Further, the treatability of wood (Tripathi and Poonia, 2015) and its suitability to plywood (Uday et al., 2011) were explored in a few studies. Researchers attempted the deployment of wood-quality traits in the selection of candidate trees for tree improvement (Chauhan and Arun Kumar, 2014). As per the available literature, the age of the wood studied for wood quality assessment is one to ten-year-old. Further, the wood of less than five-year-old trees was characterized elaborately in the literature (Saravanan et al., 2013a; Sinha et al., 2019). Few studies reported variation in vertical and lateral tree growth and also variation between trees (Chauhan and Arun Kumar, 2014; Sharma et al., 2017), which affects the realization of high-value products from fast-grown plantation timbers due to lack of homogeneity in wood. The wood of prominent plantation species like *Eucalyptus* spp., and *Acacia auriculiformis* also exhibit higher growth stress, excessive shrinkage and processing difficulties limiting their utility in solid wood products (Sharma et al., 2017). The estimated volumetric shrinkage for 5-6 and 9-10 years-old *M. dubia* wood was 17% and 20%, respectively (Sharma et al., 2019). Thus, there is a scope for characterization of *M. dubia* wood of older ages grown under various climatic regimes and management including agroforestry with and without preservation treatment to define end uses.

### *Plywood industries*

As reported, *M. dubia* wood yields type-B surface veneers by peeling, which could be dried without major defects. Panels built using urea-formaldehyde and phenol-formaldehyde adhesives exhibit good gluing and bonding properties which are ideal for Moisture-Resistant (MR) and Boiling-Water-Resistant (BWR) grade plywood (Uday et al., 2011). Further, colour variations, swirls, checks and splits were also reported. The reported combi-ply built by sandwiching one to three veneers between facial layers of *M. dubia* and *Populus deltoides* in combinations, exhibited glue shear strength enough to pass Indian Standard Specification (IS:303) in dry and wet conditions (Ismita and Shilpa, 2015). However, five-layer combi-ply at wet conditions reportedly failed in standard examination (Ismita and Shilpa, 2015). Thus, further research is required for improving the quality and durability of wood composites and engineered wood of *M. dubia.*

Tripathi and Poonia (2015) observed cracks and splits in felled logs soon after harvest and suspected growth stresses for such deformities. However, measured growth-strain (mean, $< 360 \times 10^{-6}$), in *M. dubia* plantation of Punjab and Karnataka was within the threshold limit ($700 \times 10^{-6}$) which indicates no end-splitting in logs and warping in timber (Sharma et al., 2017). Further, no warping and bowing were observed in boards made from four-year-old wood but poor stiffness (Sharma et al., 2017). Nonetheless, *M. dubia* wood is classified as moderate to non-durable wood (Nazma et al., 1981; Ruwanpathirana 2014). Contrary results merit further research to explain *M. dubia* wood traits.

*Pulp and paper industry*

The studied physical, chemical properties and strength of one to five-year-old wood suggest harvesting at the age of four or five years to obtain suitable quality wood for pulp and paper industries (Saravanan et al., 2013a; Sinha et al., 2019). Moderate lignin content, acceptable holocellulose, pulp yield, kappa number, tensile, tear and burst index (Saravanan et al., 2013a) agrees with the requisite quality. However, Chinnaraj and Malimuthu (2011) rejected *M. dubia* as pulpwood by citing low bulk density which in turn results in low throughput in fibre line. Such contrasting results merit further evaluation of *M. dubia* wood.

This leads to speculation that the growing conditions had an influence on the wood qualities. The studies reported 450 - 575 kg/m$^3$ basic density for wood of more than four years old trees (Nazma et al., 1981; Saravanan et al., 2013a; Chauhan and Arun Kumar, 2014). However, the recorded wood density of *M. dubia* in the world wood density database is in the range of 284 to 400 kg/m$^3$ (Reyes et al., 1992; Zanne et al., 2009). Thus, it merits a research exploration for defining the suitability of *M. dubia* wood for the paper and pulp industry and to create market for wood generated through thinning and pruning of plantations which in turn ensures early income to the planters.

*Wood qualities concering wood fuel and biomass-based energy plants*

Evaluation of wood for its fuel properties ensures possible wood utility in biomass-based energy plants and most particularly in cooking hearths of rural India (Chinnaraj and Malimuthu, 2011; Saravanan et al., 2013c). The reported calorific value of *M. composita* wood is 5043 – 5176 k cal (Tripathi and Poonia, 2015) which is much higher than 3820 k cal recorded by burning five - year age-old *M. dubia* wood (Saravanan et al., 2013c). Further, *M. dubia* grown in Southern Karnataka exhibits gradual improvement in fuel properties of wood over the ages (Saravanan et al., 2013c). Therefore, reported low and high calorific values, calls for a re-evaluation of wood of different age class and across locations as wood properties vary with growing conditions and age.

### 2.1.5. Wood seasoning and preservation

Wood seasoning and preservation are essential to ensure the durability of wood in outdoor conditions. The Wood of *M. dubia* with ~ 22% shrinkage warrants proper seasoning (Sharma et al., 2012). In literature, studies dealing particularly with seasoning of *M. dubia* wood are very scarce, however, a study (Tripathi and Poonia, 2015) dealing with the preservation of *M. dubia* wood by impregnating copper-chrome-arsenate and Zinc copper borate composition reveals that wood seasons well in fresh wood, but develops end–splitting and discolour when stacked in the air for a longer period (Tripathi and Poonia, 2015). It is reported that the penetration and retension of the preservatives varies across pith, heartwood and sapwood and thus wood was placed in treatability class C with 21– 42% penetration and profuse longitudinal gush (Tripathi and Poonia, 2015). In contrast, Ruwanpathirana (2014) reported that *M. dubia* wood could easily be treated with boron preservatives. Nevertheless, the information on seasoning, preservation and resultant wood durability is very scarce in the available literature.

### 2.1.6. Supporting genetics and tree improvement research

Genetic diversity within and between families (Kumar et al., 2013; Rawat et al., 2016), was studied for guiding the selection of superior trees for tree improvement programmes. In this direction, the DNA extraction method for *M. dubia* has been standardized (Rawat et al., 2016) and Random Amplified Polymorphic DNA (RAPD) marker technique was used to evaluate the genetic diversity of *M. dubia* populations in the northern Indian states of Haryana, Himachal Pradesh, Punjab and Uttarakhand. The study suggests that *M. dubia* has a narrow genetic base in Northern India (similarity indices: 0.80 – 0.91) (Johar et al., 2017). In contrast, a significant genetic variation in morphological traits was observed among the plus trees selected from open-pollinated families in the state of Tamil Nadu (Kumar et al., 2013). However, referred studies are devoid of descriptive biometrics and parentage of plus trees. A comparison of genetic variation exists in the natural stands of geographically isolated regions of India such as the Western Ghats and the Eastern Ghats and the North-Eastern regions in particular and other countries are essential to gauge the genetic variability in *M. dubia* and to exploit its genetic potential as an ideal species for tropical plantation forestry.

As a part of the tree improvement, Forest Research Institute, Dehradun, has developed ten high-yielding varieties of *M. dubia* (Kumar et al., 2017) which have mean productivity of 35 $m^3$ $ha^{-1}$ $yr^{-1}$. These varieties were developed through the selection of plus trees in Haryana, Punjab, Uttarakhand and Uttar Pradesh states of Northern India (Kumar et al., 2017). Further, the existence of sympatric and allopatric natural hybridization among the members of Meliaceae, like *Cedrela* species, demands molecular-level exploration for the identification of landraces and provenances before any irrevocable depletion of *M. dubia* gene pool in the nature (Garcia et al., 2011; Liao et al., 2016; Quiroga et al., 2016; Zelener et al., 2016), as species occurs in association with *Toona ciliate* and *Chukrasia tabularis* in natural forests (Nagalakshmi et al., 2003).

### *2.1.7. Tree propagation*

*M. dubia* tree is largely propagated through seeds. The tree bears an ovoid-shaped multi-carpel drupe. It has a skinny exocarp, filled with pulpy mesocarp and stony endocarp. Usually packed with one to six black coated seeds in separate locules (Suresh, 2013). Since the 1970s, many researchers tried to address poor seed germination in *M. dubia* (< 5%), which is mainly attributed to impermeable endocarp and recognized as one of the major hindrances to establishing large-scale *M. dubia* plantations (Nasayao et al., 1994; Nair et al., 2005). Many kinds of pre-sowing treatments were tested, for instance light-fire scorching, soaking in water and slaked lime solutions (Vivekanandan, 1978), alternate wetting and drying, burying in the pit (Tilakaratna, 1991), soaking in farm yard manure (Vivekanandan, 1978), hot and cold treatment (Nasayao et al., 1994), mechanical scarification (Suresh, 2013), acid scarification (Nasayao et al., 1994; Suresh, 2013), cow-dung slurry treatments and growth hormone treatment (Suresh, 2013). However, the reported highest germination in all pre-sowing treatments was < 40% and many treatments failed (Camus, 2008; Suresh, 2013). In contrast, Warrier (2015) reports 60% drupe germination without any pre-treatment but by removal of water-floating drupes before sowing on a nursery bed. In fact, determination of percentage of germination on a seed basis is not possible because seeds packed tightly inside locules and it is difficult to exhume intact seeds (Tilakaratna, 1991; Suresh, 2013). Reviewed literature on germination does not provide whether entire drupe or naked seeds were used in the studies and most studies expressed germination per cent over the number of drupes sown (Tilakaratna, 1991).

It was also observed that abundant seed germination in the nature at rain-water wash-in deposit sites. Acquaint local people, particularly tribes, pricks and bag such wildings and sell them to private nurseries. Further, it was witnessed that *M. dubia* woodlots established through seeds dropped by sheep and goat herds stopped overnight on the agricultural fields. Therefore, such observations highlight gaps in understanding physiological, biochemical, thermal and seasonal climatic cues working in background for ecological regulation of germination or time required for after ripening to break dormancy in *M. dubia* seeds (Camus, 2008; Suresh, 2013).

Tilakaratna (1996) made an earlier attempt at vegetative propagation through cuttings in *M. dubia* achieving ~ 76% success in rooting without any chemical treatment under mist chamber conditions. Similarly, rooting of juvenile stem cuttings by dipping cut end in 5000 ppm IBA, resulted in 50% success (Nair et al., 2005). In order to upscale micropropagation, the mini-cutting protocol was developed and succeeded in 70% rooting and survival (Chinnaraj and Malimuthu, 2011). Many attempts were made to standardize propagation protocol by trying juvenile stems, twigs and mature branches across a varied concentration of rooting-hormone treatments (Warrier, 2011). Rooting of hardwood cutting was poor (Suresh, 2013) but juvenile stem cutting was found best, however, reported response varies with the size of cutting and growing season (Warrier, 2011). Cuttings of 15 cm length and two cm thick, prepared between May to July, were found to respond better with 55 to 60% rooting (Selvakumar et al., 2013). *M. dubia* roots sprout many suckers, thus Selvakumar et al. (2013) tried to induce and isolate root suckers, by digging a circular trench around a selected plus tree and bagging isolated suckers into growing media. Nevertheless, the reported success was merely 12%. Rooting of apical shoot cuttings, from coppice, was found poor (< 3%) and production of ramets from mature stumps was not encouraging for mass propagation (Selvakumar et al., 2013). Aseptic growing media and controlled growing conditions (thermo-regulated mist chambers) are needed to be standardized for mass propagation through vegetative methods.

Recent developments in mass propagation through tissue-culture-based micropropagation techniques promise to overcome low seed germination in tree crops. For *M. dubia*, Chinnaraj and Malimuthu (2011) developed a protocol for mass propagation of *M. dubia* through tissue culture by supplementing base Murashige and Skoog (MS) media with 6–benzylaminopurine (BAP) and auxins for initiation, multiplication, elongation and rooting of the apical meristem. This protocol was adopted for the commercial production of quality planting material. Shah *et al.* (2016) also succeeded in inducing multiple shoots from callus on BAP and NAA supplemented MS media. However, the shortcomings of micropropagation such as soma-clonal variation, lengthy hardening process and failure of propagules under field conditions are yet to be evaluated. Information on growth and wood characteristics of plantations raised from vegetative and tissue cultured plants is not found.

## 2.2. Identified research priorities for *M. dubia*

A systematic review of the literature identifies the following research gaps. Studies dealing with the growth and performance of *M. dubia* across climatic and edaphic conditions and management regimes such as planting densities and irrigation were largely absent. Despite its huge popularity, almost no attention was paid to research concerning photosynthesis and tree physiology. Additionally, the water requirement of the tree and its growth-linked hydraulic architecture of the species was not explored across its natural range. Species specific allometric local or regional growth models for estimation of aboveground and belowground biomass were also not developed. Information on species performance under mixed stands and intercropping is largely missing. Though, silvicultural practices are building up slowly based on results of past established woodlots (Warrier, 2014; Kirankumar et al., 2017) and are yet to define the standard package of production practices. The resistance to diseases and pests and the tolerance to changing climatic situations remain unaddressed. Thus, the tree improvement through selection should focus on identifying resistant local landraces having straight-bole and required wood qualities in their natural range.

## 2.3. Controls of tree aboveground biomass (*AGB*) production

The predicted frequent drought and flood events of the future climate (IPCC, 2021) demands the exploration of the climatic requirement of the species for its adoption in the future production system. Drought-induced tree mortality is expected to increase globally due to climate change (Hammond et al., 2022). Growth and biomass production in tropical trees are often largely controlled by climate and specifically by water availability, while factors such as soil or disturbance history are secondary (Toledo et al., 2011; Becknell et al., 2012; Wagner et al., 2012 and 2014; Guan et al., 2015). Therein, higher precipitation and shorter and less intense dry periods were associated with significantly higher tree growth rates, while weak or no relationships with soil nitrogen or plant-available phosphorus were found (Toledo et al., 2011). The mean annual precipitation often explains a large part of the observed variation in *AGB* or growth (Becknell et al., 2012; Wagner et al., 2012 and 2014; Guan et al., 2015). The derived variable, climatological water deficit, is also found more suitable for studying the effects of water availability on tree growth because it reflects both the duration and severity of water-limited conditions over the course of a year (Chave et al., 2014; Esquivel-Muelbert et al., 2017). Indications that water availability often is a crucial factor controlling tree growth are further strengthened by previous reports of vastly increased growth in irrigated compared to non-irrigated plantations, particularly in water-limited tropical regions (Hunter, 2001; Stape et al., 2010; Campoe et al., 2013; Pérez-Cruzado et al., 2014; Minhas et al., 2015). The review reveals that no previous studies explored the effects of natural or artificial water supply or their interaction with the growth of *M. dubia*. However, such information is essential for further improving its management, e.g., with regard to optimized site selection or drought-mitigating irrigation schemes.

Wood density (*WD*) was strongly linked with vegetation biomass production and carbon storage (Hofhansl et al., 2020) and it is an important parameter in the tree biomass estimation allometric models (Chave et al., 2014; Aabeyir et al., 2020; Hofhansl et al., 2020).

## 2.4. Study on growth determining hydraulic wood and leaf traits

Water availability controls plant productivity (Wright et al., 2001; Guan et al., 2015; Berner et al., 2017) and which also varies with the water transport capacity of the xylem (Poorter et al., 2010; Hoeber et al., 2014; Kotowska et al., 2021). Plants can achieve higher xylem conductivity by producing wider vessels. The classic principle of plant hydraulic architecture postulates that the wood of trees growing in dry environments is composed of smaller xylem conduits than the wood of trees in wet environments (Carlquist, 1977; Chenlemuge et al., 2015; Pfautsch et al., 2016). According to the most recent understanding, water limitation does not *per se* result in the formation of smaller xylem conduits, but does affect the growth rate and tree height (Lechthaler et al., 2019; Fajardo et al., 2020). Because the flow path length, i.e. the distance from the apex towards the stem base, strongly affects vessel dimensions at the stem base (Olson et al., 2021), many previous reports of differing vessel dimensions across sites might simply reflect different tree heights. Hence, recent studies have emphasized the role of tree size (particularly distance from the apex to the stem base) and cambial age in the comparability and interpretation of hydraulic-climate relationships (Rosell et al., 2017; Li et al., 2019; Soriano et al., 2020), highlighting the need to compare branches of similar size and from a similar canopy position to reduce the influence of vertical or radial gradients when studying trees exposed to different environmental conditions (cf. Petit et al., 2016).

A coordinated trade-off between xylem hydraulic properties and leaf functional traits is expected (Brodribb, 2009). High hydraulic efficiency has been found to be essential to maintaining high transpiration and carbon gain rates per unit of leaf area (Zhang et al., 2016). Further, a high specific leaf area (*SLA*) has been associated with low carbon investment per wood volume (Poorter et al., 2010), while leaf-to-sapwood area ratios are linked to a habitat’s hydroclimate (Martinez-Vilalta et al., 2009; Gleason et al., 2016; Anderegg et al., 2021). Thereby, intraspecific adjustments along water availability gradients rely on changes in resource allocation between sapwood and leaf area (Mencuccini et al., 2019; Rosas et al., 2019).

In order to increase yield in drought-prone environments, it has been recommended to irrigate forest plantations (Armitage, 1985). So far, the influence of irrigation on tree hydraulics traits is less well-explored than vascular adjustments along natural water availability gradients. Studies on current year branches of seasonally irrigated olive trees (Torres-Ruiz et al., 2013) and young willows (Achinelli et al., 2018), however, reported no marked variation in conduit diameter and density, potentially because the flow path length was unaffected. Along with irrigation, nutrient availability also enhances tree productivity (Stape et al., 2010; Campoe et al., 2013; Pérez-Cruzado et al., 2014). The increased availability of nutrients positively impacts average vessel diameter, resulting in higher specific conductivity and increased growth rates (Hacke et al., 2017). Nonetheless, tree hydraulic research frameworks dealing with responses to drought have largely focused on water and carbon associated mechanisms, whereas the role of nutrients is often overlooked (Gessler et al., 2017). Indeed, semi-arid tropical regions tend to have low soil fertility (Wani et al., 2011) while humid tropical lowland ecosystems are relatively rich in available $N_{\mathrm{soil}}$ (Vitousek, 1984; Sollins, 1998) and growth rate is likely to be limited by $P_{\mathrm{soil}}$ or other rock-derived nutrients (Tanner et al., 1998).

Despite the increasing popularity of *M. dubia* in farm and agroforestry and its extensive distribution across hydroclimatic regimes, to our knowledge studies related to its hydraulic architecture so far are missing. Given the importance of an efficient hydraulic system for plant biomass accumulation (cf. Tyree, 2003; Brodribb, 2009), it is important to understand the variability of the hydraulic architecture of *M. dubia* across a wide range of environmental conditions.

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# Chapter 3: Methods

# 3. Methods

## 3.1. Overall research process

The research work carried out for this dissertation involves two-stage sampling for two different studies related to (1) determination of factors controlling tree growth across rainfall gradients and (2) exploration of variation in growth-determining hydraulic wood and leaf traits in *M. dubia*. Separate methodologies were adopted for each study. The first study mainly focuses on climatic, soil and management factors that influence biomass production in *M. dubia*. The second study examined the variability in stem anatomy linked to hydraulic wood and leaf traits in *M. dubia* across a steep water availability gradient. The detailed account of materials and methodologies adopted in this investigation presented in the following subheads.

## 3.2. Study area

The study was conducted in South India (Fig. 3.1). The sampling plots are spread over Andhra Pradesh, Karnataka and Tamil Nadu state in the region and fall within latitude of 11° 8' 49.992" and 15° 44' 3.084" N and the longitude of 74° 53' 17.016" and 77° 51' 9.108" E. Plots were identified across precipitation gradient of 400 mm $yr^{-1}$ at interior peninsular India to more than 3000 mm $yr^{-1}$ towards the Western Ghats. Tropical monsoon climate prevails in the region, with a rainy season from May to October and a dry season from November to April. Mean annual temperature (*MAT*) ranges from 29.5 °C in the inland lowlands to 21.6 °C in the highlands (Ghats) (Fick and Hijmans, 2017).

## 3.3. Study on determination of tree aboveground biomass and its controls

Methods adopted in determining the controls of tree biomass growth, are presented in the following section.

### *3.3.1. Study sites*

Study sites were identified through expert discussion with staff of the Karnataka Forest Department, forestry colleges and research institutes, NGOs, nursery enterprises, media personnel and farmers. Based on expert opinion and field inspections, study sites were selected in the region. An extensive field inventory was conducted in 186 woodlots which were aged between approx. one to nine years during the field survey in 2017 and older stands were not found in the region. The woodlots spread across the mean annual precipitation (*MAP*) gradient of 420 to 2170 mm $yr^{-1}$ (Fig. 3.1). *M. dubia* is commonly not grown at higher rainfall levels. The gradient encompasses four climatic zones (arid, semi-arid, dry-sub-humid and humid; zonation according to Trabucco and Zomer 2019).

### *3.3.2. Land-use history and management*

Land-use history and management information of each selected woodlot was collected by interviewing farmers with semi-structured questionnaires (Fig. 3.2a). All selected *M. dubia* woodlots were established on former agricultural land. At the beginning of the *M. dubia* cultivation, all interviewed farmers irrigated the seedlings for at least one growing season to avoid early-stage failures. About 63 farmers managed woodlots under rainfed conditions after the initial irrigation period (Fig. 3.2c) but 123 farmers continued supplementary water application for more than one growing season, however, with reduced irrigation frequencies (Fig. 3.2d). *MAP* at all non-irrigated woodlots was higher than 670 mm $yr^{-1}$.

### *3.3.3. Plot design and tree observations*

The plots of 20 m × 20 m were established near the centre of the woodlots to avoid edge effects, at locations typical for the average growth conditions of the woodlot (based on visual assessment and discussion with the owner) and tree biometric data were collected (Fig. 3.2b). All the trees with a diameter at breast height (*DBH*, cm) equal to or larger than 2 cm and whose center points lay within the plot boundaries were recorded as sample trees. Stand density (trees $ha^{-1}$) was estimated from the number of recorded trees per 400 $m^2$ plot. For each sample tree, DBH was measured with a diameter tape and height (m) was measured using a marked PVC pipe for smaller trees and a Vertex IV hypsometer (Haglöf, Langsele, Sweden) for trees higher than approx. 8 m. A total of 6898 *M. dubia* trees were recorded across the studied woodlots.

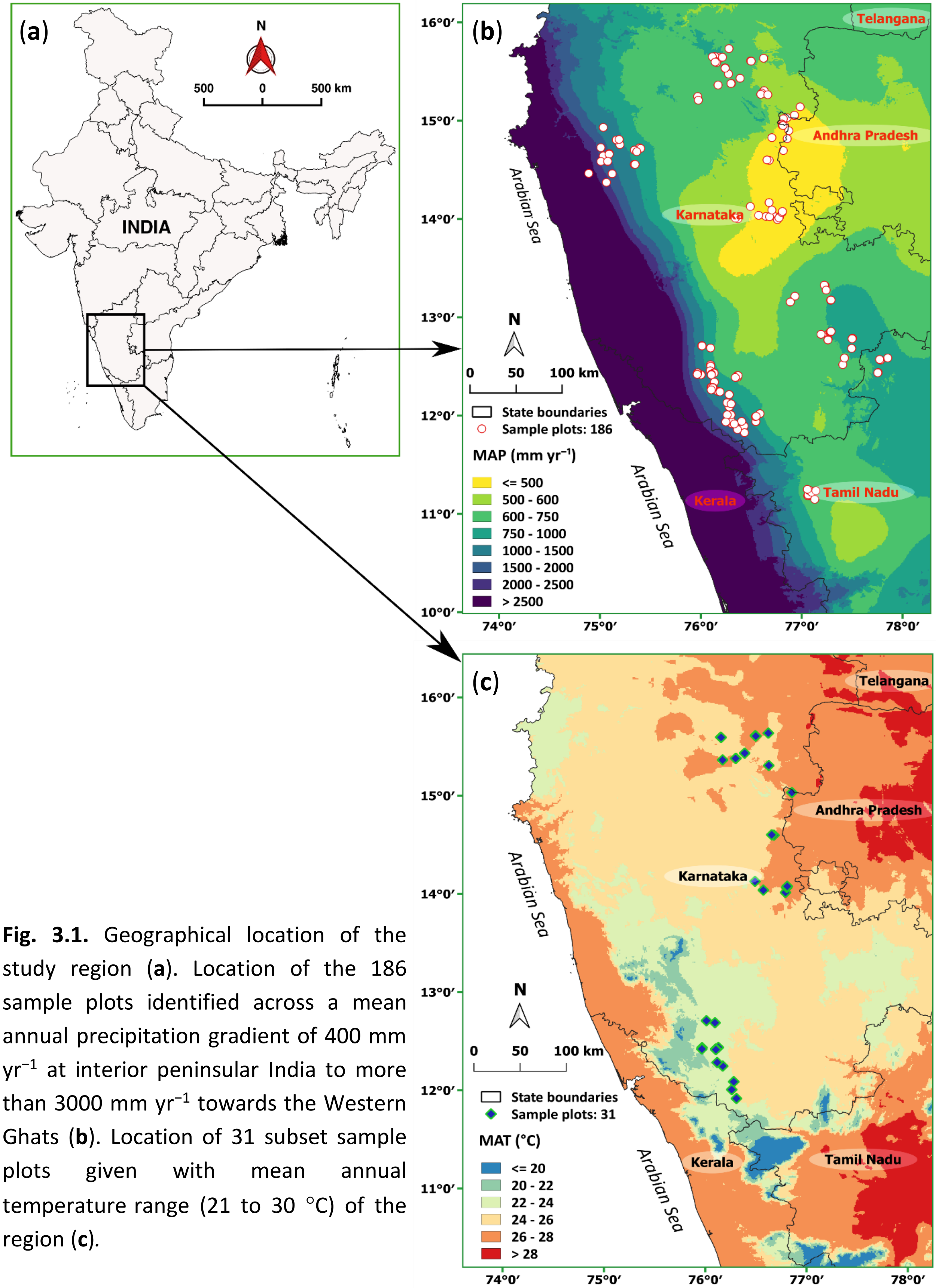

**Fig. 3.1.** Geographical location of the study region (**a**). Location of the 186 sample plots identified across a mean annual precipitation gradient of 400 mm yr$^{-1}$ at interior peninsular India to more than 3000 mm yr$^{-1}$ towards the Western Ghats (**b**). Location of 31 subset sample plots given with mean annual temperature range (21 to 30 °C) of the region (**c**).

**Fig. 3.2.** Field inventory: collection of land-use history and management information (**a**), laying of a study plots in the plantation (**b**) and data collection at non-irrigated site (**c**). Irrigated plot showing with rolled-up drip-laterals hanged over tree trunks (**d**).

### *3.3.4. Aboveground biomass model selection*

For estimating tree-level aboveground biomass (*AGB*, kg tree$^{-1}$), no allometric equation specifically calibrated for *M. dubia* was available from existing literature. Thus, an improved pan-tropical allometric model (Chave et al., 2014) was used in the study to predict *AGB* based on wood density (*WD*) (g cm$^{-3}$), *DBH* (cm) and tree height, *H* (m):

$$AGB = 0.0673 \times (WD \times DBH^2 \times H)^{0.975} \tag{3.1}$$

To ascertain the applicability of the model to the plantation crops in general and the *M. dubia* woodlots in particular, the reviewed literature revealed that the model was applied widely for estimating the *AGB* of tropical trees including plantation species such as *Eucalyptus*, *Gmelina* *arborea* and *Tectona grandis* (Sales-come and Baldos, 2018; Osuri et al., 2020; Tesfaye et al., 2020). Further, its pantropical predecessor (Chave et al., 2005), was also applied for *AGB* estimation in a *Melia azedarach* plantation (Rahman et al., 2016). Additionally, a reported species-specific form factor (0.7) based volume equation (Nuthan et al., 2009) was used with *WD,* estimated in the study (0.35 g $cm^{-3}$) and a generally reported wood specific gravity (*WSG*, 0.4). Other potentially suitable equations (Brown et al., 1989; FSI, 1996; Aabeyir et al., 2020) were also deployed for *AGB* estimation and derived estimates were compared (Table 3.1) and correlated with Chave et al. (2014) (Fig. 4S3). Though, the comparison of models with the pantropic models of Chave et al. (2014) using a paired *t*-test on *AGB* estimates of 6898 tress revealed significant difference ($p < 0.001$, Table 3.1), the *AGB* values derived with the improved pan-tropical model for *M. dubia* correspond very closely to values derived with Nuthan et al. (2009), having only marginal divergences from the 1:1 line and close correlation ($R = 1$, Fig. 4S3b). Other suitable equations deployed were also produced comparable absolute estimates and close correlations ($R > 0.9$, Fig. 4S3c-e).

### 3.3.5. Wood density estimation

For wood density (*WD*; g $cm^{-3}$) estimation, stem wood cores were collected from a subset of 31 woodlots, which covering a *MAP* gradient from 420 to 1530 mm $yr^{-1}$ (Fig. 3.1b) and a plantation age gradient from four to seven years. One wood core each was extracted at breast height (1.3 m, see Fig. 3.3) from the six trees that were closest to the center of a given plot and hence total 186 cores collected. The fresh volumes (*v,* $cm^3$) of the cores were determined by Newton's volume equation:

$$v = [(A_o + 4A_m + A_i)/6] \times l \tag{3.2}$$

where $A_o$, $A_m$ and $A_i$ are the cross-sectional areas obtained by $A = \pi D^2 /4$, using the diameter (*D*, cm) measured at outer end, middle and inner end of the core, and $l$ is the core length (cm), all measured with a digital caliper (Mitutoyo, Japan). Wood density was calculated as the ratio of oven-dry mass (105 °C for 72 h) and fresh volume of each core.

The average *WD* derived from the 31-plot subsample was 0.349 ± 0.003 g $cm^{-3}$ (mean ± *SE*, n = 186 trees), with a range from 0.253 to 0.435 g $cm^{-3}$. This falls into the range of *WD* estimates previously reported for *M. dubia* (Reyes et al., 1992; Zanne et al., 2009; Chauhan and Arun Kumar, 2014). *WD* showed no or only weak correlations ($R < 0.22$) with the available stand, management, climate and soil variables (see overview in Table 4S1), and linear regressions between *WD* and selected key variables show either no significant influence on *WD* ($p > 0.05$) or did not explain a sufficiently large fraction of the variance in the variable ($R^2 < 0.05$) to use them to predict *WD* (Fig. 4S2a-f). We therefore decided to use the overall average of *WD* for the aboveground biomass estimates at all woodlots in our study.

**Fig. 3.3.** Extraction of stem cores in the field using an increment borer having 5.15 mm inner diameter (Haglöf, Sweden) (**a**). Extracted wood core(s) (**b**) were preserved in 50% ethanol for wood anatomical studies (**c**).

### *3.3.6. Bioclimatic Variables*

The bioclimatic variables used in the study were extracted from WorldClim database (Version 2, http://worldclim.org). The point sampling tool of QGIS software (QGIS, 2017) was used for extracting nineteen bioclimatic variables data for each woodlot from available global grids. The database provides monthly long-term (1970–2000) average data at a spatial resolution of 30 arc seconds (Fick and Hijmans, 2017). Additionally, monthly potential evapotranspiration (*PET*, mm) and aridity index estimates were extracted from 30 arc seconds resolution global raster grids (Trabucco and Zomer, 2019). Further, number of dry months per year at each site was computed by combining the extracted monthly precipitation (WorldClim) and *PET* (CGIAR-CSI) data series following an approach by Guan et al. (2015), where dry months are defined as months in which PET exceeds precipitation. Another variable, climatological water deficit (*CWD*, mm $\text{yr}^{-1}$) was derived by following Chave et al. 2014, where the annual *CWD* is the sum of the differences between monthly precipitation (WorldClim) and monthly PET (CGIAR-CSI), taking into consideration only months with negative values. A list of all available climate variables is presented in Table 4S1.

### 3.3.7. Soil Variables

Soil texture was assessed by the 'finger probe' field method (Thien, 1979), as modified by USDA (www.nrcs.usda.gov). Near the center of each plot, soil pH was recorded using a handheld pH/ORP meter (GMH 5530, Greislinger, Regenstauf, Germany) by dissolving 20 g of soil in 50 mL of distilled water. Similarly, soil electrical conductivity (dS $\text{m}^{-1}$) was measured using the Fieldscout EC 110 Meter (Spectrum Technologies Inc., Aurora, USA). For each plot, a composite soil sample was prepared from five field samples extracted at 0–15 cm depth. Samples were air-dried and passed through a 2 mm sieve to determine available soil nutrient contents. The content of organic carbon ($OC_{\text{soil}}$) was estimated by rapid titration method using 1 g of sample sieved through 0.2 mm mesh (Walkley and Black, 1934). Available soil nitrogen ($N_{\text{soil}}$, mg $\text{kg}^{-1}$) was determined by the alkaline permanganate method (Subbiah and Asija, 1934), available phosphorus ($P_{\text{soil}}$, mg $\text{kg}^{-1}$) by Olsen's method using ascorbic acid (Olsen, 1954) and available potassium ($K_{\text{soil}}$, mg $\text{kg}^{-1}$) was determined with the flame photometer method using ammonium acetate extracts (Richards, 1954). Soil depth was approximated by measuring the distance from the top of the soil to the bedrock in existing pits, trenches or channels dug in the plots for planting or other purposes. A list of all available soil variables is compiled in Table 4S1.

### 3.3.8. Data analysis and model building

To determine the relationships between stand-level *AGB* and potential explanatory variables, correlation was computed. Among the forty odd variables, a set of weakly correlated predictor variables were selected based on a priori knowledge about their association with plant growth.

**Table 3.1.** Comparison of results of applied *AGB* models with the Chave et al. (2014) model using paired *t*-test.

| Methods | *WD* /*WSG** | Mean | *SD* | *SE* | *CI* | *p*-value | Models | FF | Shortcomings |
|---|---|---|---|---|---|---|---|---|---|
| Chave et al. 2014 | *WD:* 0.35 | 33.02 | 40.24 | 0.48 | 0.95 | < 0.001 | $AGB = 0.0673 \times (WD \times (DBH)^2 \times H)^{0.975}$ |  | For FF estimation, measurements, data and average value of trees in region were not given in the report |
| Nuthan et al. 2009 | *WSG*: 0.4 | 36.43 | 45.46 | 0.55 | 1.07 |  | $v = BA \times H \times FF$ | 0.7 |  |
| Difference |  | -3.41 | -5.23 | -0.06 |  |  |  |  |  |
| Nuthan et al. 2009 | *WD:* 0.35 | 31.88 | 39.78 | 0.48 | 0.94 | < 0.001 | $v = BA \times H \times FF$ | 0.7 | ” |
| Difference |  | 1.14 | 0.46 | 0.00 |  |  |  |  |  |
| Aabeyir et al. (2020) | *WD*: 0.35 | 33.36 | 41.59 | 0.50 | 0.98 | < 0.001 | $AGB = 0.0580 \times wd \times ((DBH)^2 \times H)^{0.999}$ | -- | Followed Chave et al. (2014) and updated for tropical woodlands of Ghana |
| Difference |  | -0.34 | -1.35 | -0.02 |  |  |  |  |  |
| Chave et al. (2005) | *WD:* 0.35 | 29.68 | 34.85 | 0.42 | 0.82 | < 0.001 | $AGB = 0.0776 \times (wd \times DBH^2 \times H)^{0.940}$ | -- | Developed with small data set as compared to Chave et al. (2014) |
| Difference |  | 3.34 | 5.39 | 0.06 |  |  |  |  |  |
| Brown et al. (1989) |  | 40.99 | 48.95 | 0.59 | 1.15 | < 0.001 | $AGB = 34.4703 - (8.0671 \times DBH) + 0.6589 \times DBH^2$ | -- | Single variable, *DBH* based model. Overestimates *AGB* for trees. Height of trees is ignored |
| Difference |  | -7.97 | -8.71 | -0.11 |  |  |  |  |  |
| FSI 1996 | *WSG*: 0.4 | 48.55 | 22.30 | 0.27 | 0.53 | < 0.001 | $v = 0.16948 - 1.85075 \times DBH + 10.63682 \times DBH^2$ | -- | Single variable, *DBH* based. Overestimates *AGB* for smaller *DBHs* and underestimates *AGB for* bigger *DBH* trees. Height of trees is ignored |
| Difference |  | -15.53 | 17.94 | 0.21 |  |  |  |  |  |

*SD*: standard deviation; *SE*: standard error; *CI*: confidence interval; *FF*: form factor; *WD*: wood density (g $cm^{-3}$); *WSG*: wood specific gravity; *BA*: basal area ($m^2$); *DBH*: diameter at breast height (cm); *H*: height (m). **WD* and *WSG* used to convert estimated volume into *AGB* (kg)

The modelling process on the stand-level *AGB* increment in *M. dubia* was began fitting a simple regression between *AGB* (Mg $ha^{-1}$) and stand age. It was found that the power-law relationship between the *AGB* of plot *i* and its age (months since planting) to fit the data best. Further model expression was linearized through natural log-transformation of *AGB* and stand age. To examine the effects of management, climate and soil on *AGB* and *AGB* increment, an extended version of simple regression model was fitted with an expresses of baseline biomass only depends on the initial planting density, while the effects of water availability, soil nutrients and potential negative density-dependent effects on growth manifest their influence on biomass via the growth rate. Additionally, to account effect of irrigation on sites that have a more negative water balances, interaction between *CWD* and the categorical management variable irrigation was allowed into the final multiple linear regression model. The detailed information on the models built for identifying the controls of *AGB*, data transformation, scaling centering and visualization were given in the Chapter 4.

## 3.4. Study on growth-determining hydraulic wood and leaf traits

### *3.4.1. Study sites*

A subset of 31 plantations (Fig. 3.1c), from which stem cores were collected for wood density estimation (see section 3.3.5), were selected for studying growth-determining hydraulic wood and leaf traits. The age of the plantation, prevailing bioclimatic conditions and management practices adopted in the plantations were given in the chapter 5.

### *3.4.2. Environmental variables*

Bioclimatic variables for the location of each woodlot was extracted from the CHELSA database (Version 1.2, http://chelsa-climate.org, Karger et al., 2017) using the R packages raster (Hijmans, 2020) and sp (Bivand et al., 2013). The data are provided as monthly averages for the years 1979–2013 at a spatial resolution of 30 arc seconds. Further, monthly *PET* (*ET*0, mm) and annual aridity index (*AI*) were extracted from Climate Database as defined in previous study. The *CWD*, (mm $yr^{-1}$) was calculated according to Chave et al. (2014) and was used as a proxy for water stress. All the four soil properties ($OC_{soil}$ (% mass), $N_{soil}$, (mg $kg^{-1}$), $P_{soil}$, (mg $kg^{-1}$) and $K_{soil}$, (mg $kg^{-1}$)) estimated from a composite soil sample, were added to the data set to explore the influence of soil.

### *3.4.3. Biometric data and plant material*

Within the selected 31 plots, six representative trees per plot were chosen for biometric data and plant material collection (Fig. 3.4a, b). Thus, the field inventories were conducted on 186 trees in total during July and September 2017. The subsample of trees for wood anatomical and hydraulic measurements was chosen by stratifying the trees in each plot by their diameter and selecting six individuals with a diameter close to the plot average and approximately equidistant to the plot center (Fig. 3.4a). For the estimation of biomass, the height (H, 6.3 – 19.2 m) was measured with a Vertex IV hypsometer (Haglöf, Sweden), and the diameter at breast height (DBH, 8.11 – 31.5 m) was determined with diametric tape at 1.3 m height for each of the selected trees. Sun-exposed branches were cut from each tree using a long-reaching pruner (Fig. 3.4c) to obtain leaf (Fig. 3.4d) and branch (Fig. 3.4e-f) samples for morphological, chemical and anatomical analyses.

### *3.4.4. Wood density and biomass production*

Methods adopted for wood density presented in previous section 3.3.5 and for estimation of *AGB* (kg) of each tree was extracted using R package BIOMASS (Réjou-Méchain et al., 2017), which was again based on improved pan-tropical allometric model (Eq3.1) given by Chave et al. (2014).

### *3.4.5. Leaf morphological and chemical traits*

Leaf morphological traits such as mean leaf area ($A_{\mathrm{leaf}}$, $cm^2$), specific leaf area (*SLA*, $cm^2\ g^{-1}$) and branch-total leaf area ($cm^2$, *SLA* × dry mass of all leaves (g) were estimated. The leaf-to-sapwood area ratio ($A_l{:}A_s$, $m^2\ cm^{-2}$) was also computed using the xylem area of the branches ($A_{\mathrm{xylem}}$, $mm^2$). In addition, foliar signatures of $\delta^{13}C$ and $\delta^{15}N$ were also recorded. The detailed methodology adopted for estimation of above traits were given in the chapter 5.

### *3.4.6. Branch and stem xylem anatomy and hydraulics*

The basipetal branch segments, from which leaf samples were collected for studying leaf morphological and chemical traits, were excised for branch anatomical analysis (Fig. 3.4e, f). Semi-thin transverse sections were cut using a sliding microtome (G.S.l.1, Schenkung Dapples, Zürich, Switzerland, see Fig. 3.5 a). Six sections per branch were stained with Safranin-Alcian Blue and mounted on glass slides (Fig. 3.5c, d). An image of a section was digitally captured at 100× magnification in the stereomicroscope fitted with a digital camera and an automatic mobile stage (see, Fig. 3.5b, SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany). Captured images were processed using Adobe Photoshop CS6 (Version 13.0 × 64, Adobe Systems Incorporated, USA) and ImageJ v1.47v. Similar to the branch samples, the wood cores used for wood density measurement were first re-hydrated in a water bath for a day, and then sectioned radially (30–40 µm) by using a sliding microtome for stem wood anatomical analyses.

Like branch sections, four sections per core were stained, mounted and dried before capturing an image with the stereomicroscope. To keep a uniform area of measurement, only 20 mm length (from outer bark end to inner pith end) of the captured images was processed per sample. The particle analysis function of ImageJ was used to estimate single and cumulative vessel lumen area and vessel density (branch and stem $VD$, n mm$^{-2}$). Equivalent vessel diameter ($D$, µm) was calculated for each vessel following White (2006). Relative vessel lumen area ($A_{\mathrm{lumen}}$, %), i.e. the lumen-to-sapwood area ratio (percentage of cumulative vessel lumen area ($A_{\mathrm{lumen}}$, mm$^2$) of the total xylem area ($A_{\mathrm{xylem}}$, mm$^2$)) was derived. Single branch and stem vessel diameters ($D$, µm) were used to calculate hydraulically weighted vessel diameter ($D$h, µm) following Sperry et al. (1994). The theoretical hydraulic conductivity ($K_{\mathrm{h}}$, kg m MPa$^{-1}$ s$^{-1}$) was calculated according to the Hagen–Poiseuille equation. From that, the theoretical sapwood area-specific and leaf area-specific hydraulic conductivity (branch and stem $K_{\mathrm{p}}$ and $K_{\mathrm{l}}$, m$^{-1}$ MPa$^{-1}$ s$^{-1}$) were subsequently calculated by dividing $K_{\mathrm{h}}$ by the branch or stem core xylem area ($A_{\mathrm{xylem}}$, m$^2$) and leaf area ($A_{\mathrm{l}}$, m$^2$), respectively.

### 3.4.7. *Data analysis and model building*

All statistical analyses were performed in R (v. 4.0.4; R Core Team, 2021). In order to analyze the joint effect of climate, irrigation treatment, soil properties and biometric traits on a series of tree properties while simultaneously accounting for random plot differences, mixed effects models were fitted using R package lme4 (Bates et al., 2015). All strictly positive variables were natural log transformed to ensure normality of residuals. All numeric variables were subsequently scaled and centered to ease the comparison of regression parameters. Reduced set of variables were deployed in the models to derive the effect of climate, soil and management on tree growth, anatomic and hydraulic traits. To reduce the number of variables in the model (cf. Fig. 5S1), we decided a priori to limit the analysis of soil variables to nitrogen and phosphorus content (two important indicators of soil nutrient availability), and to use the climatological water deficit (which integrates both precipitation- and temperature-related components of climatic water availability) as the sole predictor of climatic water availability. Further details of methods were given in the Chapter 5.

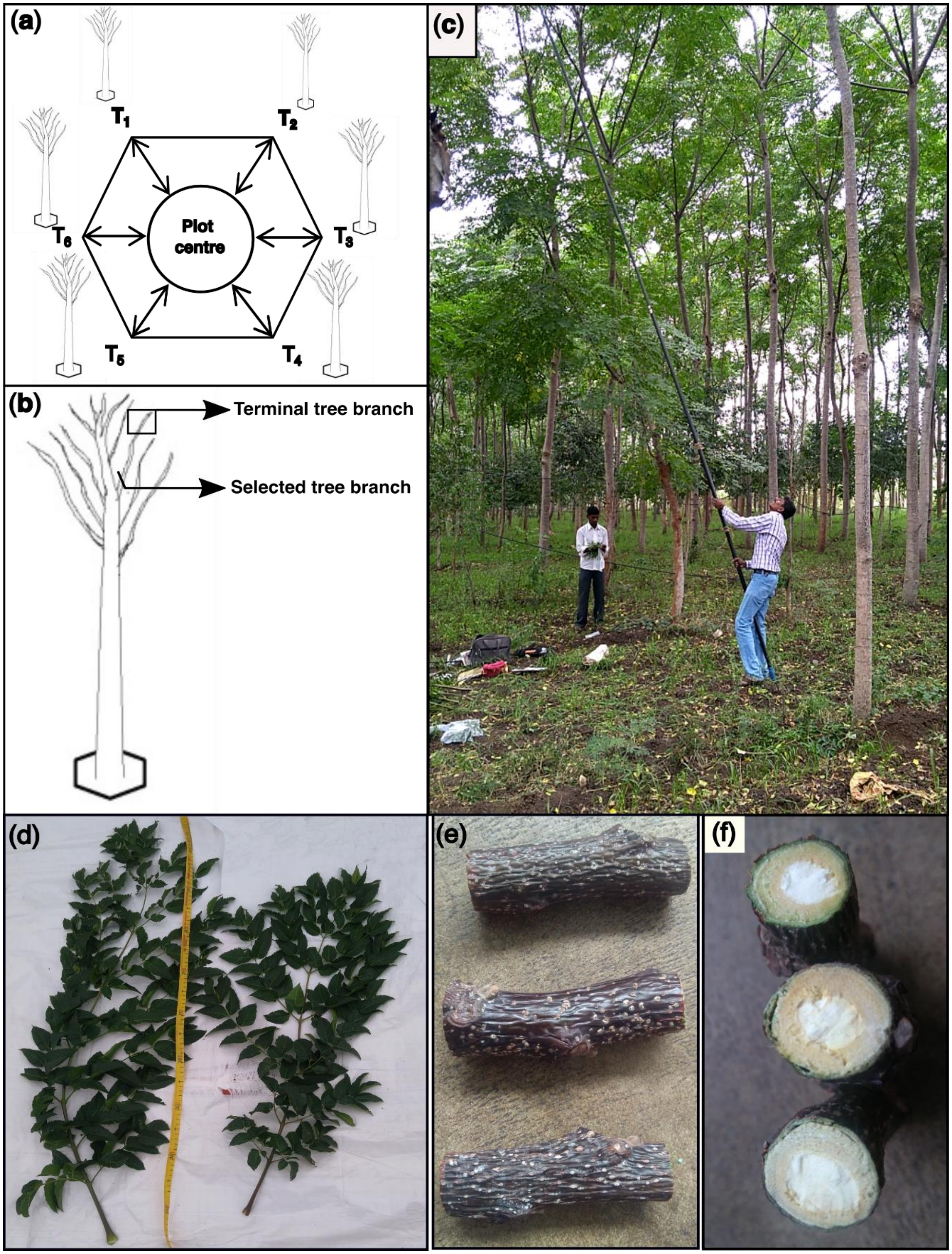

**Fig. 3.4.** Schematic representation of tree selection in the sample plot for biometric data collection (**a**) and selection of branch (**b**) for plant material collection. $T_1$ to $T_6$ denotes selected trees. A photo showing branch sample collection scheme adopted in the field (**c**), leaf (**d**) and terminal branches (**e** and **f**).

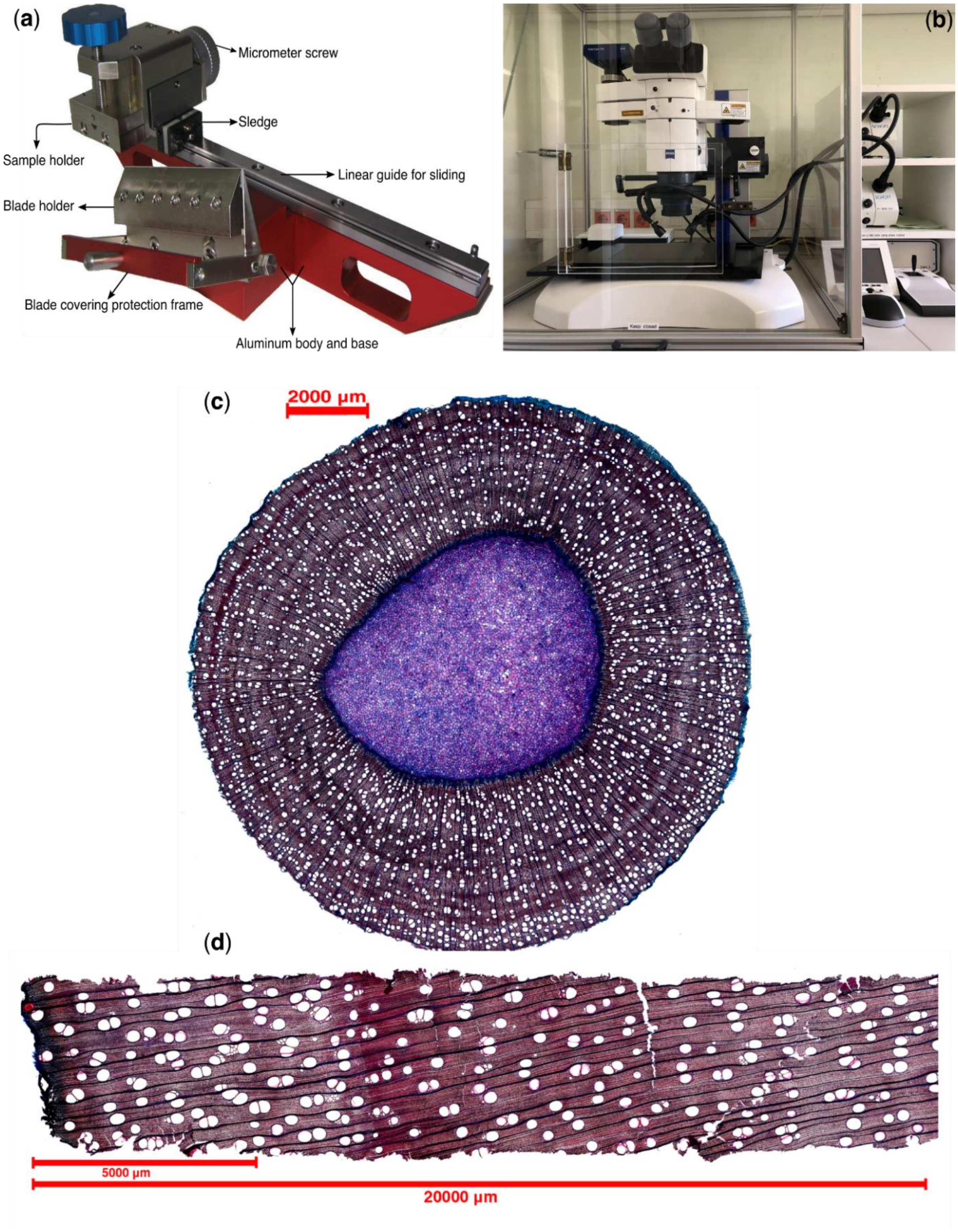

**Fig. 3.5.** A sliding microtome (**a**) and stereomicroscope fitted with a digital camera and an automatic mobile stage (**b**) used in the study. Semi-thin transverse section of branch (**c**) and stem cores (**d**) stained with Safranin-Alcian Blue.

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# Chapter 4: Water availability controls the biomass increment of *Melia dubia* in south India

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# 4. Water Availability Controls the Biomass Increment of *Melia dubia* in South India

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### Abstract

Farmland tree cultivation is considered an important option for enhancing wood production. In South India, the native leaf-deciduous tree species *Melia dubia* is popular for short-rotation plantations. Across a rainfall gradient from 420 to 2170 mm $yr^{-1}$, we studied 186 farmland woodlots between one and nine years in age. The objectives were to identify the main factors controlling aboveground biomass (*AGB*) and growth rates. A power-law growth model predicts an average stand-level *AGB* of 93.8 Mg $ha^{-1}$ for nine-year-old woodlots. The resulting average annual *AGB* increment over the length of the rotation cycle is 10.4 Mg $ha^{-1}$ $yr^{-1}$, which falls within the range reported for other tropical tree plantations. When expressing the parameters of the growth model as functions of management, climate and soil variables, it explains 65% of the variance in *AGB*. The results indicate that water availability is the main driver of the growth of *M. dubia*. Compared to the effects of water availability, the effects of soil nutrients are 26% to 60% smaller. We conclude that because of its high biomass accumulation rates in farm forestry, *M. dubia* is a promising candidate for short-rotation plantations in South India and beyond.

**Keywords:** aboveground biomass, climatological water deficit, farm forestry, farmland woodlots, rainfall gradient, soil; wood production.

## 4.1. Introduction

Increasing landscape tree cover and carbon sequestration is considered a cost-effective climate change mitigation tool. While natural secondary succession of native forest tree species is likely the preferred option from an ecological point of view, agroforests, farm woodlots and tree plantations are land-use options that can balance ecological and socio-economic needs (Ghazoul et al., 2019; Guariguata et al., 2019; Lewis et al., 2019; Dave et al., 2019). They are considered particularly important regarding the extent and further expansion of global drylands (Maestre et al., 2012; Huang et al., 2016; Bastin et al., 2017). Fast-growing short-rotation plantations constitute one potentially important component of future climate-smart 'designer landscapes' (see, e.g., (Koh et al., 2009)), particularly in tropical regions with climatically favorable conditions for fast growth. They can shift pressure from remaining forests and help to meet the booming wood demand in fast-emerging economies (FAO and UNEP, 2020).

A prime example is India, which houses nearly 18% of the global human population on 2.4% of the world's land area (UN, 2019). Its economic growth and increasing population are associated with an increasing demand for wood and wood-based products (Singh et al., 2012; World Bank, 2021). In 2019, India imported 8.7 billion USD worth of wood products (Fig. 4S1) (FAO, 2021). The further projected high economic growth rate (OECD, 2018), continued population growth (World Bank, 2021) and forest policy reforms are expected to create substantial additional demand for wood-based products in the coming years (Ghosh and Sinha, 2016). An additional, intrinsic value of landscape tree cover may further arise from future ecosystem service payment schemes for carbon storage or other protective purposes.

Tree plantations in India and elsewhere in the tropics are often established from a very limited number of 'classic', highly productive plantation species (Lamb et al., 2005; FAO, 2010, Amazonas et al., 2018; Liu., et al., 2018). Within relatively short rotation cycles, which vary among species but are often around ten years, substantial aboveground biomass (*AGB*) is accumulated. For example, an *AGB* of about 140 Mg ha$^{-1}$ was reported for nine-year-old *Eucalyptus tereticornis* plantations in India (Rawat and Negi 2004). There are, however, controversies about potential negative impacts of some introduced plantation species on soil, water and biodiversity (Hughes, 1994; Joshi and Palanisami, 2011; Bilal et al., 2014). This has led to a ban of *Eucalyptus* and *Acacia* plantations in some southern states of India (GOK, 2017).

Among the tree species commonly used for plantation establishment in India, the native *Melia dubia* Cav. (Meliaceae) is gaining popularity due to its fast growth, straight boles and self-pruning, and its ability to cope with different edaphic and climate conditions (Nasayao et al., 1994; Sharma et al., 2012). It occurs naturally in the moist tropical forests of peninsular and northeastern India and can also be found, either naturally or introduced, in Sri Lanka, Malaysia, Indonesia, the Philippines, Australia and Ghana (Wunder etal., 2012; Thakur et al., 2020). *M. dubia* is a light-demanding, deciduous tree species (Warrier, 2011; Nguyen et al., 2014) and its wood is suitable for plywood, paper and engineered wood industries (Parthiban et al., 2009; Sinha et al., 2019; Thakur et al., 2020). However, studies on *AGB* and the growth of *M. dubia* are rare so far, and with exception of one study on the effects of varying stand densities (Kirankumar and Patil, 2017), its growth potential has not yet been assessed comprehensively across gradients in water and nutrient availability.

For tropical trees, several studies reported that biomass and growth are often largely controlled by climate and specifically by water availability, while factors such as soil or disturbance history are secondary (Toledo et al., 2011; Becknell et al., 2012; Wagner et al., 2012 and 2014; Guan et al., 2015). Therein, higher precipitation and shorter and less intense dry periods were associated with significantly higher tree growth rates, while weak or no relationships with soil nitrogen or plant available phosphorus were found (Toledo et al., 2011). The climatic variable mean annual precipitation often explains a large part of the observed variation in *AGB* or growth (Becknell et al., 2012; Wagner et al., 2012 and 2014; Guan et al., 2015); however, the variable climatological water deficit is deemed even more suitable for studying the effects of water availability on growth because it reflects both the duration and severity of water-limited conditions over the course of a year (Chave et al., 2014; Esquivel-Muelbert et al., 2017). Indications that water availability often is a crucial factor controlling tree growth are further strengthened by previous reports of vastly increased growth in irrigated compared to non-irrigated plantations, particularly in water-limited tropical regions (Hunter, 2001; Stape et al., 2010; Campoe et al., 2013; Pérez-Cruzado et al., 2014; Minhas et al., 2015). To our knowledge, no previous studies investigating effects of natural or artificial water supply or their interaction on the growth of *M. dubia* are available. However, such information is essential for further improving its management, e.g., with regard to optimized site selection or drought-adapted irrigation schemes.

*M. dubia* is particularly popular in South India, a region characterized by a tropical monsoon climate with a distinct seasonality and steep gradients in annual rainfall. On South Indian farms, we studied 186 *M. dubia* farmland woodlots between one and nine years in age and covering a rainfall gradient from 420 to 2170 mm $\mathrm{yr}^{-1}$. The objectives were to quantify aboveground biomass and growth rates of *M. dubia* and to identify their main controlling factors, with a focus on the role of natural and artificial water supply and their interaction.

## 4.2. Materials and Methods

### *4.2.1. Study region*

The studied woodlots were located in the South Indian states of Andhra Pradesh, Karnataka and Tamil Nadu (Fig. 4.1). Tropical monsoon climate prevails in the region, with a rainy season from May to October and a dry season from November to April. Mean annual precipitation (*MAP*) increases from the interiors with around 400 mm $\mathrm{yr}^{-1}$ towards the Western Ghats with more than 3000 mm $\mathrm{yr}^{-1}$ (Fig. 4.1). Mean annual temperature (*MAT*) ranges from 29.5 °C in the inland lowlands to 21.6 °C in the highlands (Ghats) (Fick and Hijmans, 2017). The soils in the region are variable (Bhattacharyya et al., 2013) and accommodate diverse vegetation formations ranging from open thorn scrub over wooded grasslands to closed forests (Roy et al., 2015; Ratnam et al., 2019). The region has a long-standing history of diverse land-use practices; coffee, coconut, areca nut and rubber plantations dominate in the moist, humid and sub-humid zones, whereas rainfed and irrigated agriculture dominates in the dry lowland plains (Roy et al., 2015). Today, forest cover in the region is about 14% (GOI, 2019).

### *4.2.2. Study Sites and Plot Design*

The woodlots ranged from approx. one to nine years in age; older stands were not found in the region. The woodlots covered a gradient in *MAP* from 420 to 2170 mm $\mathrm{yr}^{-1}$ (Fig. 2); *M. dubia* is commonly not grown at higher rainfall levels. The gradient encompasses four climatic zones (arid, semi-arid, dry-sub-humid and humid; zonation according to Trabucco and Zomer (2019). The plots were identified and located based on information from the Karnataka Forest

Department, forestry colleges and research institutes, NGOs, nursery enterprises, media and farmers.

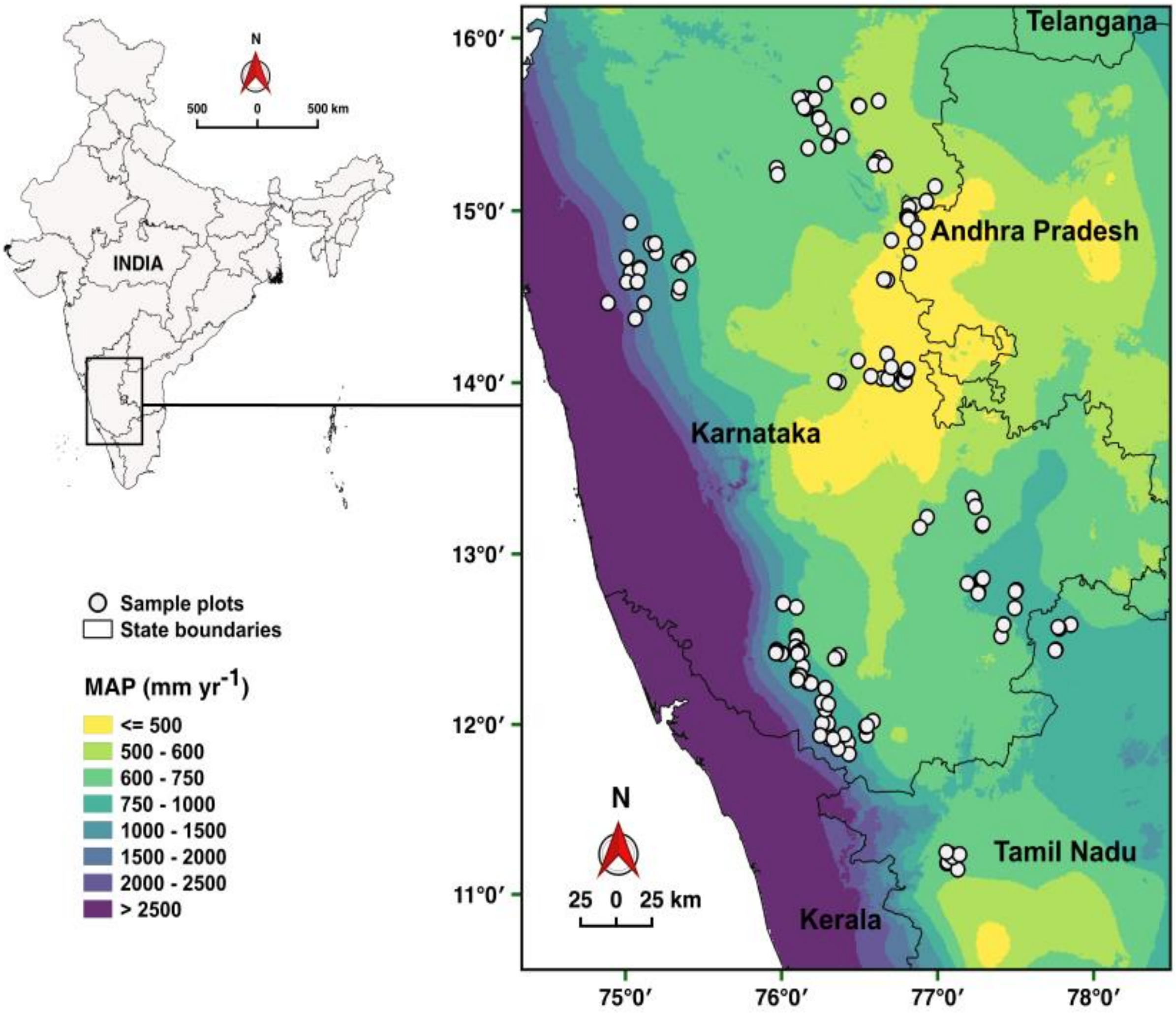

**Fig. 4.1.** Study region in South India and location of the 186 *M. dubia* woodlots. The sites span across a gradient in mean annual precipitation (*MAP*) ranging from 420 to 2170 mm yr$^{-1}$.

General land-use history and management information on each woodlot were raised through interviewing farmers with semi-structured questionnaires. All studied *M. dubia* woodlots were established on former agricultural land. To avoid early-stage failures of the woodlots, all interviewed farmers irrigated the seedlings for at least one growing season. Most farmers (66%) continued supplemental irrigation for more than one growing season, but with reduced irrigation frequencies (hereafter referred to as 'irrigated'). A total of 34% moved to exclusively rainfed cultivation after the initial irrigation period (hereafter referred to as 'non-irrigated');

*MAP* at all non-irrigated woodlots was higher than 670 mm $yr^{-1}$. In each woodlot, biometric data were collected within a 20 m × 20 m plot. The plots were established near the center of the woodlots to avoid edge effects, at locations typical for the average growth conditions (based on visual assessment and discussion with the owner).

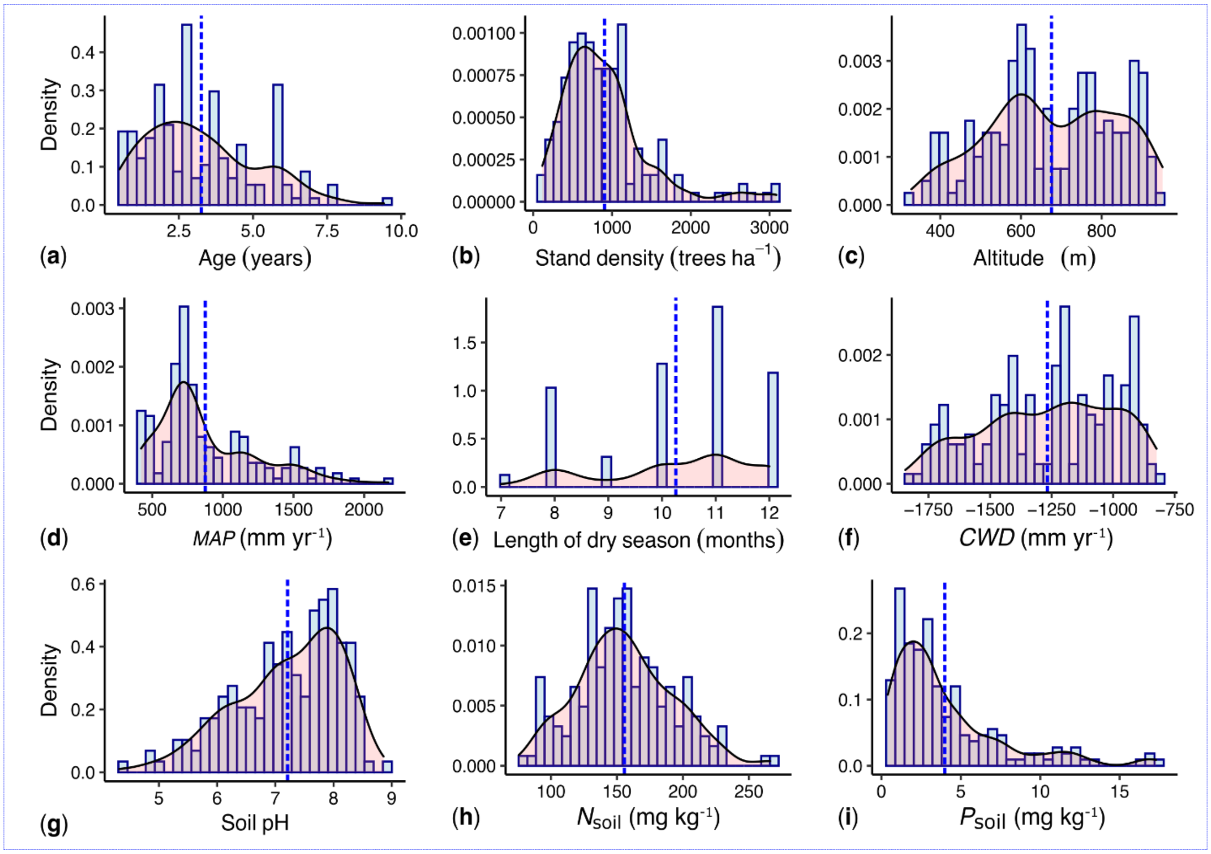

**Fig. 4.2.** Key characteristics of the studied *M. dubia* woodlots. Histograms and kernel densities of selected key sites and management (**a–c**), climate (**d–f**) and soil variables (**g–i**) along the studied gradients. *MAP*: Mean annual precipitation; *CWD*: climatological water deficit; $N_{soil}$: soil nitrogen content; $P_{soil}$: soil phosphorous content.

### *4.2.3. Tree Observations*

Trees with a diameter at breast height (*DBH*, cm) equal to or larger than 2 cm whose center-points lay within the plot boundaries were recorded as sample trees. Stand density (trees $ha^{-1}$) was estimated from the number of recorded trees per 400 $m^2$ plot. For each sample tree, DBH was measured with a diameter tape and height (m) was measured using a marked PVC pipe for smaller trees and a Vertex IV hypsometer (Haglöf, Langsele, Sweden) for trees higher than approx. 8 m. A total of 6898 *M. dubia* trees were recorded across the studied woodlots.

### 4.2.4. Wood density

On a subset of 31 woodlots covering a *MAP* gradient from 420 to 1530 mm $yr^{-1}$ and a plantation age gradient from four to seven years, stem wood density (*WD*; g $cm^{-3}$) was additionally measured. In these plots, one wood core each was extracted at breast height (1.3 m) from the six trees that were closest to the plot center, adding up to 186 cores. Volumes ($cm^3$) of the cores were determined by Newton's volume equation:

$$v = [(A_o + 4A_m + A_i) \div 6] \times l \tag{1}$$

where $v$ is the volume of the core, $A_o$, $A_m$ and $A_i$ are the cross-sectional areas obtained by $A = \pi D^2/4$, using diameter ($D$, cm) measured at outer, middle and inner end of the core, and $l$ is the core length (cm). *WD* was calculated as the ratio of oven-dry mass (105 °C for 72 h) to fresh volume of each core.

The average *WD* derived from the 31-plot subsample was 0.349 ± 0.003 g $cm^{-3}$ (mean ± SE, n = 186 trees), with a range from 0.253 to 0.435 g $cm^{-3}$. This falls into the range of *WD* estimates previously reported for *M. dubia* (Reyes et al., 1992; Zanne et al., 2009; Chauhan and Arun Kumar, 2014). *WD* showed no or only weak correlations ($R < 0.22$) with the available stand, management, climate and soil variables (see overview in Table 4S1), and linear regressions between *WD* and selected key variables show either no significant influence on *WD* ($p > 0.05$) or did not explain a sufficiently large fraction of the variance in the variable ($R^2 < 0.05$) to use them to predict WD (Fig. 4S2 a-f). We therefore decided to use the overall average of *WD* for the aboveground biomass estimates at all woodlots in our study.

### 4.2.5. Aboveground Biomass Estimation

For estimating tree-level aboveground biomass (*AGB*, kg $tree^{-1}$), no allometric equation specifically calibrated for *M. dubia* was available from existing literature. We thus used an improved pan-tropical allometric model (Chave et al., 2014), which predicts *AGB* (kg) based on *WD* (g $cm^{-3}$), *DBH* (cm) and tree height, *H* (m):

$$AGB = 0.0673 \times (WD \times DBH^2 \times H)^{0.976} \quad (2)$$

The model is widely applied for estimating the *AGB* of tropical trees including plantation species such as *Eucalyptus*, *Gmelina arborea* and *Tectona grandis* (Sales-come et al., 2018; Osuri et al., 2020; Tesfaye et al., 2020). Its pantropical predecessor (Chave et al., 2005), which yields slightly lower but highly correlated estimates ($R$ = 1, Fig. 4S3a), was previously applied for *AGB* estimation in a *Melia azedarach* plantation (Rahman et al., 2016). The *AGB* values derived with the improved pan-tropical model for *M. dubia* correspond very closely to values derived with an approach using a reported species-specific form factor of 0.7 (Nuthan et al., 2009), along with mean *WD* as established in our study, with only marginal divergences from the 1:1 line and close correlation ($R$ = 1, Fig. 4S3b). Other potentially suitable equations for tropical trees also produce comparable absolute estimates and close correlations (n = 6898 trees, $R > 0.9$, Fig. 4S3c-e). A species-specific model calibration in future studies would most likely improve the accuracy of predictions, foremost by a more precise estimation of the wood volume for given age classes, as *WD* did not vary across gradients of key management, climate and soil variables in our study (Fig. 4S2). The target variable, stand-level *AGB* (Mg ha$^{-1}$) was determined by multiplying the mean tree level *AGB* of a given plot by the respective stand density (trees ha$^{-1}$).

### 4.2.6. Bioclimatic Variables

We used the point sampling tool of QGIS software (QGIS, 2017) for extracting bioclimatic data for each woodlot from available global grids. We extracted variables related to precipitation and temperature from the WorldClim database (Version 2, http://worldclim.org, accessed on 20 June 2021). The data are provided as monthly long-term averages (1970–2000) at a spatial resolution of 30 arc seconds (Fick and Hijmans, 2017). We further extracted monthly potential evapotranspiration (*PET*, mm) and aridity index estimates from 30 arc seconds resolution global raster grids (Trabucco and Zomer, 2019). We derived the number of dry months per year at each site by combining the extracted monthly precipitation (WorldClim) and *PET* (CGIAR-CSI) data series following an approach by Guan et al. (2015), where dry months are defined as months in which *PET* exceeds precipitation. We further calculated the climatological water deficit (*CWD*, mm $yr^{-1}$) following Chave et al. (2014), where the annual *CWD* is the sum of the differences between monthly precipitation (WorldClim) and monthly *PET* (CGIAR-CSI), taking into consideration only months with negative values. For the modeling in our study, we chose the annual *CWD* as the climatic variable as it integrates both the duration and severity of water-limited conditions over the course of a given year (Chave et al., 2014; Esquivel-Muelbert et al., 2017)).

Calculating climate variables specifically for the growing season of *M. dubia* was not possible due to a lack of information on the expected substantial changes in the phenology of *M. dubia* as a drought-deciduous species along the steep climatic gradient. A list of all available climate variables is presented in Table 4S1.

### *4.2.7. Soil Variables*

Soil texture was assessed by the 'finger probe' field method (Thien, 1979), as modified by www.nrcs.usda.gov. Near the center of each plot, soil pH was recorded using a handheld pH/ORP meter (GMH 5530, Greislinger, Regenstauf, Germany) by dissolving 20 g of soil in 50 mL of distilled water. Similarly, soil electrical conductivity (dS $m^{-1}$) was measured using the Fieldscout EC 110 Meter (Spectrum Technologies Inc., Aurora, USA). In each plot, a composite soil sample was extracted at 0–15 cm depth and air-dried. Samples were passed through a 2 mm sieve to determine available soil nutrient contents in the laboratory of the Indian Institute of Soil and Water conservation, Ballari, India. The content of organic carbon ($OC_{soil}$) was estimated by rapid titration method using 1 g of sample sieved through 0.2 mm mesh (Walkley and Black, 1934). Available soil nitrogen ($N_{soil}$, mg $kg^{-1}$) was determined by the alkaline permanganate method (Subbiah and Asija, 1934), available phosphorus ($P_{soil}$, mg $kg^{-1}$) by Olsen's method using ascorbic acid (Olsen, 1954) and available potassium ($K_{soil}$, mg $kg^{-1}$) was determined with the flame photometer method using ammonium acetate extracts (Richards, 1954). Soil depth was approximated by measuring the distance from the top of the soil to the bedrock in existing pits, trenches or channels dug in the plots for planting or other purposes. A list of all available soil variables is compiled in Table 4S1.

### 4.2.8. Statistical Analyses

To identify relationships between our target variable stand-level *AGB* and potential explanatory variables, we computed a correlation matrix with the R package ggcorrplot (Version 0.1.3, (Kassambara, 2019). Out of the list of more than 40 available stand, management, climate and soil variables (Table 4S1, Fig. 4S4), we chose a limited set of weakly correlated predictor variables based on a priori knowledge about their association with plant growth.

To model the stand-level *AGB* increment in *M. dubia* in the studied woodlots, we first fitted a simple regression model between *AGB* (Mg $ha^{-1}$) and stand age. We found a power-law relationship between the *AGB* of plot *i* and its *age* (months since planting) to fit the data best:

$$AGB_i = a \times age_i^{b} \tag{3}$$

This model can be linearized by natural log-transforming *AGB* and stand age:

$$\text{Log}\,(AGB_i) = \log(a) + b \times \log\,(age_i\,) + \epsilon_i \tag{4}$$

On the scale of the raw data, fitting a log-log linear model as in (4) with a simple linear model corresponds to a power-law relationship of *AGB* with age, and a lognormal error distribution.

To examine the effects of management, climate and soil on *AGB* and *AGB* growth, we further fitted an extended version of model (3) that expresses the baseline $a_i$ and growth rate $b_i$ for observation *i* as functions of stem density, water availability and soil nutrients:

$$a_i = a_0 \times exp\,(a_1 \times density_i) \tag{5}$$

$$b_i = b_0 + b_1 \times density_i + b_2 \times irrigation_i + b_3 \times CWD_i + b_4 \times N_{soil[i]} + b_5 \times P_{soil[i]} + b_6 \times CWD_i \times irrigation_i \tag{6}$$

We therein assumed that the baseline biomass *a* only depends on the initial planting density, while the effects of water availability, soil nutrients and potential negative density- dependent effects on growth manifest their influence on biomass via the growth rate *b*. As the effect of irrigation is likely more pronounced on sites that have a more negative water balance, we further allowed for an interaction between climatological water deficit and the categorical management variable, irrigation. On the log-log scale, the model implied by (-3), (-5) and (6) can be expressed as a multiple linear regression model:

$$\log(AGBi) = \log(a_0) + a_1 \times \log(density_i) + b_0 \times \log(age_i) + b_1 \times density_i \times \log(age_i) + b_2 \times irrigation_i \times \log(age_i) + b_3 \times CWD_i \times \log(age_i) + b_4 \times N_{\mathrm{soil}[i]} \times \log(age_\mathrm{i}) + b_5 \times P_{soil[i]} \times \log(age_i) + b_6 \times CWD_i \times irrigation_\mathrm{i} \times \log(age_i) + \epsilon_i \tag{7}$$

To fit model (7), all numeric predictor variables except the (negative) *CWD* were natural log-transformed in order to accommodate the skew of the data. Except for age, all numeric predictors were then scaled by their standard deviations and centered around zero to ease the interpretation of model coefficients. To visualize the results of the multiple regression model, we computed partial predictions for the key variables *CWD*, stand density, $N_\mathrm{soil}$ and $P_\mathrm{soil}$ along their respective observed ranges (rescaled to original units) for both irrigated and non-irrigated woodlots while keeping all other variables at their average values (see Table 4S1). All statistical analyses and plotting were performed using R (Version 4.0, (R Core Team, 2020). We used the open source software Inkscape (Version 1.0, (Inkscape, 2020)) for aesthetic adjustments on figures.

## 4.3. Results

The studied woodlots were vastly heterogeneous with regard to management, climate and soil conditions (Fig. 4.2). A total of 66% of the woodlots were irrigated (vs. 34% non-irrigated). Stand densities varied 26-fold, from 116 to over 3000 trees $\mathrm{ha}^{-1}$. *MAP* ranged from 420 to 2170 mm $\mathrm{yr}^{-1}$ and the *CWD* from –1823 to –832 mm $\mathrm{yr}^{-1}$. $N_\mathrm{soil}$ and $P_\mathrm{soil}$ varied by three- and forty-fold, respectively.

Across all woodlots, stand-level *AGB* varied from 0.3 to 110.4 Mg $\mathrm{ha}^{-1}$. Variables that could potentially explain the high observed variance in *AGB* were plotted in a correlation matrix; stand age had the highest independent correlation with *AGB* ($R = 0.55$, Fig. 4S4). A log-log linear regression model using age as a predictor explained 55% of the variance in *AGB* (*F*-statistic: 225.4 on 1 and 184 *DF*, $p < 0.001$) (Fig. 4.3). It predicted an *AGB* of 94 Mg $\mathrm{ha}^{-1}$ for nine-year-old *M. dubia* stands, which corresponded to an average annual *AGB* increment of 10.4 Mg $ha^{-1}$ $yr^{-1}$.

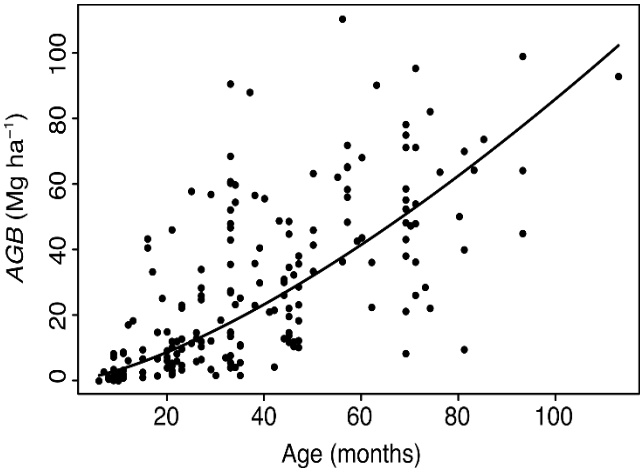

**Fig. 4.3.** Stand-level aboveground biomass (*AGB*, Mg $ha^{-1}$) vs. stand age (months) across the 186 studied woodlots. The line shows the predictions of a log-log linear regression ($R^2 = 0.55$, *F*-statistic: 225.4 on 1 and 184 *DF*, $p < 0.001$). Prediction model: *AGB* = 0.12 × age1.42, valid for an age range from 1 to 108 months.

The updated growth model taking into account the effects of management, climate and soil explained 65% of the observed variance in *AGB* (*F*-statistic: 41.6 on 8 and 177 *DF*, $p < 0.001$) (Table 4.1). Stand density had a marginally significant positive effect on initial *AGB* ($p = 0.068$) and a non-significant negative effect on aboveground biomass increment (*AGBI*). Water availability had a much stronger positive effect on *AGBI* than nutrient availability, as indicated by the larger standardized effect sizes of irrigation (0.061, $p = 0.096$) and *CWD* (0.078, $p < 0.01$) compared to $N_{soil}$ (0.031, $p = 0.107$) and $P_{soil}$ (0.045, $p < 0.01$). The three-way interaction term between stand age, *CWD* and irrigation indicates a slight but non-significant reduction in the irrigation effect at wetter sites ($p = 0.173$).

Using the model to predict the stand-scale *AGB* of ‘mature’ (harvest-ready, nine-year old) woodlots illustrates the important role of water availability. For non-irrigated mature woodlots of otherwise average characteristics, *AGB* more than triples along the steep *CWD* gradient, from 44.4 Mg $ha^{-1}$ to 150.3 Mg $ha^{-1}$. The relationship is non-linear, with smaller increases in *AGB* per unit of *CWD* at the dry end of the gradient (Fig. 4.4a). Along the same *CWD* range, *AGB* in irrigated woodlots increases by only 60% and almost linearly. While an almost twice as high *AGB* is predicted for irrigated woodlots at very negative *CWD*, *AGB* predictions for irrigated and non-irrigated woodlots are similar at the wet end of the gradient past approx.

$-1000$ mm $yr^{-1}$. Along the observed gradients in stand density, $N_{soil}$ and $P_{soil}$, *AGB* increases of 90% to 147% are predicted for non-irrigated mature woodlots of otherwise average characteristics; the model predicts 31% higher *AGB* at a given stand density, $N_{soil}$ or $P_{soil}$ when the woodlots are irrigated (Fig. 4.4b-d). However, all described trends for irrigated woodlots are associated with substantial additional uncertainties due to the large standard errors of the two interaction terms involving irrigation (Table 4.1).

## 4.4. Discussion

### *4.4.1. Aboveground Biomass of M. dubia*

In South India, the native *M. dubia* is a popular plantation species due to its versatile use, fast growth, straight boles and its ability to cope with different edaphic and climate conditions (see Fig. 4.5, Nasayao et al., 1994; Sharma et al., 2012). On farmland woodlots across large gradients in management, climate and soil conditions, our regression model predicts an average stand-level *AGB* of 93.8 Mg $ha^{-1}$ for nine-year-old *M. dubia* stands. At this age, trees are commonly harvested, and we did not observe any older stands across the studied woodlots. Predictions from our regression model for a hypothetic landscape with a homogeneous distribution of *M. dubia* plantations across nine age classes (i.e., one to nine years in steps of one year, then immediate harvest and replanting) yield an average *AGB* stock of 44.1 Mg $ha^{-1}$.

Assuming a carbon content of *AGB* of approx. 50% (Thomas and Martin, 2012), this corresponds to an average permanent aboveground carbon stock of 22.1 Mg $ha^{-1}$. In comparison, dry forests in South India were reported to have aboveground carbon stocks of 37 to 116 Mg $ha^{-1}$ (Mani et al., 2007; Naveenkumar et al., 2017; Kothandaraman et al., 2020). Such carbon stock quantifications may be of interest for life cycle analysis of *M. dubia* products, carbon offset programs or other climate change mitigation mechanisms.

**Table 4.1.** Results of the multiple regression model for stand-level aboveground biomass (*AGB*) using stand age and preselected key management, climate and soil variables and their interactions as predictors. *AGB* and predictors (except irrigation, *CWD*) were natural log-transformed. Except for the main predictor, age, numeric variables were scaled by their standard deviations and centered around zero. The model explains 65% of the variance in *AGB* across the studied woodlots (*F*-statistic 41.6 on 8 and 177 *DF*, $p < 0.001$). *CWD*: climatological water deficit; $N_{\text{soil}}$: soil nitrogen content; $P_{\text{soil}}$: soil phosphorus content.

| **Parameters** | **Estimate** | **SE** | ***t* statistic** | ***P*-value** |
|---|---|---|---|---|
| Intercept | 4.52 | 0.32 | 14.27 | <0.001 |
| Age | 1.45 | 0.09 | 16.28 | <0.001 |
| Stand density | 0.54 | 0.29 | 1.84 | 0.06 |
| Age: Stand density | -0.07 | 0.09 | -0.83 | 0.40 |
| Age: Irrigation (irrigated) | 0.06 | 0.04 | 1.67 | 0.09 |
| Age: *CWD* | 0.08 | 0.03 | 2.62 | <0.01 |
| Age: $N_{\text{soil}}$ | 0.03 | 0.02 | 1.62 | 0.10 |
| Age: $P_{\text{soil}}$ | 0.05 | 0.02 | 2.89 | <0.01 |
| Age: *CWD*: Irrigation (irrigated) | -0.05 | 0.03 | -1.37 | 0.17 |

### *4.4.2. Growth Potential of M. dubia*

Of central interest for short-rotation plantation species is their growth, i.e., their average annual *AGBI* over a typical rotation cycle. Based on the *AGB* estimate for an average nine-year old woodlot from our simple regression model, the mean *AGBI* across our study region is 10.4 Mg $ha^{-1}$ $yr^{-1}$. This estimate falls within the range of values reported for four-year-old *M. dubia* plantations in South India (9.6 to 12.7 Mg $ha^{-1}$ $yr^{-1}$, estimates derived in analogy to our study using *DBH* and height data; see Table 4S2 for details on all cited studies) (Kirankumar and Patil, 2017). The *AGBI* rate of *M. dubia* is comparable to or higher than those reported for several other popular plantation species across India. This includes reports from teak (*Tectona grandis*) of varying ages (2.6 to 16 Mg $ha^{-1}$ $yr^{-1}$, (Karmacharya and Singh, 1992; Buvaneswaran et al., 2006), five- to eleven year-old *Populus deltoides* (6.3 to 16.4 Mg $ha^{-1}$ $yr^{-1}$, (Kanime et al., 2013; Arora et al., 2014), four- to six-year-old *Gmelina arborea* (0.6 to 8.5 Mg $ha^{-1}$ $yr^{-1}$, (Swamy et al., 2003a; 2003b), three- to ten-year-old *Dalbergia sissoo* (2.5 to 7.8 Mg $ha^{-1}$ $yr^{-1}$, (Kumar et al., 1998; Hunter, 2001; Tyagi et al., 2009; Kanime et al., 2013) as well as from nine-year-old plantations of *Casuarina equisetifolia* (10.9 Mg $ha^{-1}$ $yr^{-1}$), *Pterocarpus marsupium* (7.5 Mg $ha^{-1}$ $yr^{-1}$), *Ailanthus triphysa* (4.6 Mg $ha^{-1}$ $yr^{-1}$) and *Leucaena leucocephala* (2.6 Mg $ha^{-1}$ $yr^{-1}$) (Kumar et al., 1998). Other studies on common plantation species reported higher *AGBI* (12.2 to 37.5 Mg $ha^{-1}$ $yr^{-1}$, Table 4S2) than we found for *M. dubia*, both for India (Kumar et al., 1998; Rana et al., 2001; Rajendran and Devaraj, 2004; Rawat and Negi., 2004; Minhas et al., 2015) and other tropical countries (Frederick et al., 1985a; 1985b; Wang, et al., 1991; Fuwape and Akindele, 1997). However, these studies commonly examine only one or few sites. In contrast, our average *M. dubia AGBI* estimate is based on studying 186 woodlots across steep environmental gradients. At single sites in our study, *AGBI* rates of well over 20 Mg $ha^{-1}$ $yr^{-1}$ were observed.

### 4.4.3. Controls of Biomass and Growth of M. dubia

A power-law growth curve represented the changes in *AGB* with increasing woodlot age well for the studied stands between one and nine years of age (Fig. 4.3). Our findings are in line with several previous studies in monocultural short-rotation tree plantations showing similar relationships (e.g., Paula et al., 2013; Arora et al., 2014; Minhas et al., 2015; Acuña et al., 2017).

The multiple regression model (Table 4.1) explained 65% of the observed variance in stand-scale *AGB*. It indicates a key role of water availability for the growth of *M. dubia*. Therein, both natural (*CWD*) and artificial (irrigation) water supply have strong effects on *AGB*, and the effects of irrigation vary strongly along the studied *CWD* gradient (Fig. 4.4a). The annual *CWD* was highly significant in the model (Table 4.1). Its standardized effect size on growth was 28% larger than that of irrigation and 72–150% larger than the effect sizes of $N_{soil}$ and $P_{soil}$. These results are in line with several previous studies reporting that the natural water availability is closely related to the growth of tropical trees, while soil conditions and further factors such as land-use history are often secondary (Toledo et al., 2011; Becknell et al., 2012; Wagner et al., 2012 and 2014; Guan et al., 2015).

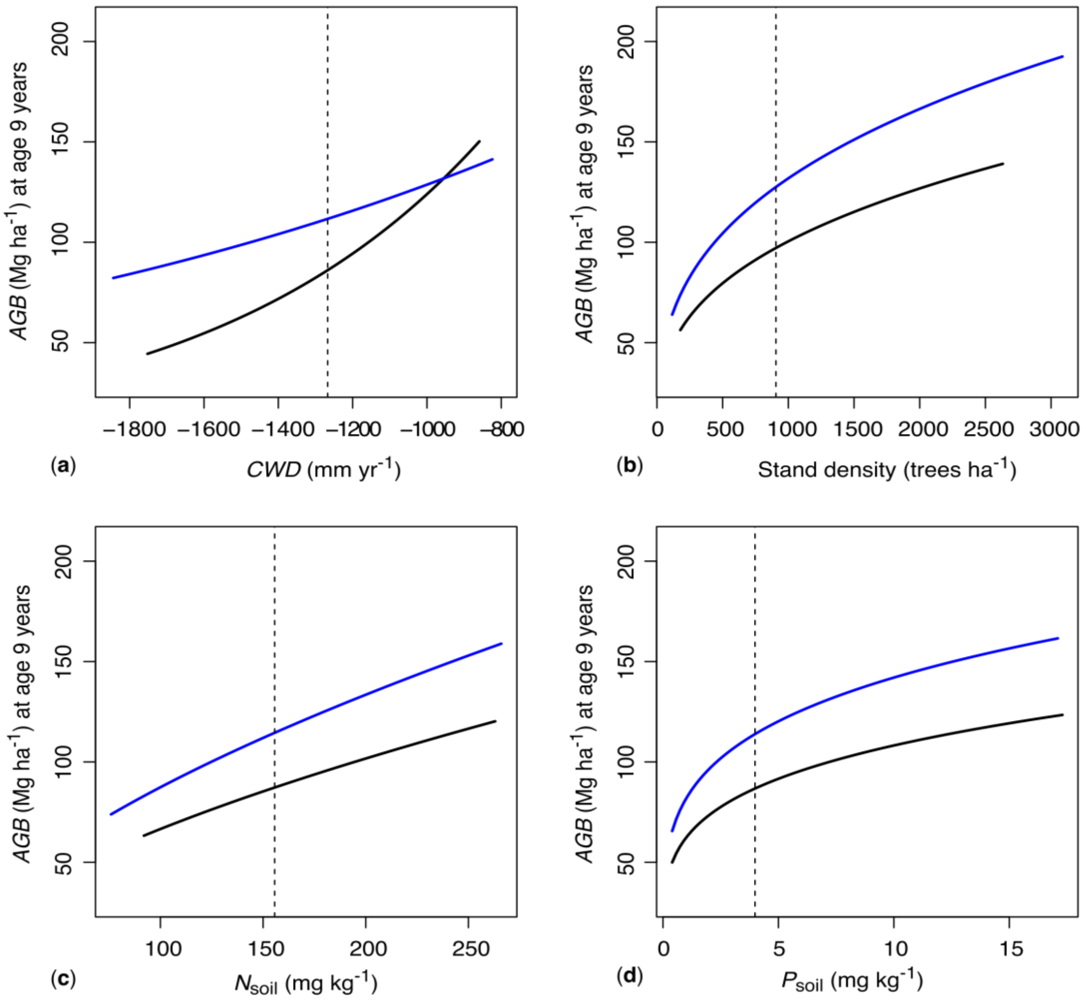

**Fig. 4.4.** Partial predictions of stand-level aboveground biomass (*AGB*, Mg ha$^{-1}$) of harvest-ready, nine-year-old woodlots as influenced by key management, climate, and soil variables. Along the observed gradients in climatological water deficit (*CWD*) (**a**), stand density (**b**) and soil nitrogen ($N_{soil}$) (**c**) and phosphorus ($P_{soil}$) (**d**), *AGB* is predicted separately for irrigated (blue lines) and non-irrigated woodlots (black lines) from the multiple model. All variables other than tree age (kept at nine years) and the respective displayed variable were kept at their average values (dashed vertical lines). Predictions were computed for the observed ranges of *CWD*, stand density, $N_{soil}$ and $P_{soil}$ in the irrigated and non-irrigated woodlots, respectively.

Likewise, the observed strong positive influence of irrigation of *AGB* growth is in line with several previous studies in tree plantations (Hunter, 2001; Stape et al., 2010; Campoe et al., 2013; Pérez-Cruzado et al., 2014; Minhas et al., 2015). Our model goes a step further in including an interaction between natural and artificial water supply, which showed an expected decreasing benefit of irrigation as the natural water availability increases (i.e., as *CWD* becomes less negative). This results in similar *AGB* predictions for mature irrigated and non-irrigated woodlots at the wet end of the studied *CWD* gradient past approx. – 1000 mm yr$^{-1}$, while an almost twice as high *AGB* is predicted for irrigated woodlots at the dry end at around –1800 mm yr$^{-1}$ (Fig. 4.4a). Such information is essential for further optimizing the growth of *M. dubia* through enhanced site selection and water management schemes.

Notably, both interaction terms involving irrigation were associated with substantial uncertainties and were thus only marginally significant and non-significant, respectively, in the multiple model (Table 4.1). There are several potential reasons for this: Firstly, there is uncertainty arising from a lack of information on irrigation frequency and volume, as irrigation only appears as a categorical variable. Secondly, first- and second-order interaction terms in general have much higher uncertainties than main effects. Thirdly, irrigation is a conscious and complex management decision by the farmers likely already taking into account local conditions and planting densities, which are not considered in our relatively simplistic model. Finally, the irrigation effect refers to a woodlot of average characteristics, i.e., at average *CWD*, while differences at the dry end of the gradient would likely be more pronounced. Despite such limitations, our model does confirm a key role of the water supply for the *AGB* growth of tropical trees, in our case for *M. dubia* in South India: growth is strongly constrained at the dry end of the studied *CWD* gradient, but can be increased considerably by irrigation.

Within the studied stand density range (116 to 3086 trees ha$^{-1}$, 67% between 116 and 1000 trees ha$^{-1}$), the model showed a marginally significant positive effect of stand density on initial *AGB* and a negative effect of stand density on *AGB* growth; the latter was nonsignificant in our model (Table 4.1). As for irrigation, a potential explanation for the lack of significant growth effects is that stand density is a management decision by farmers that is likely based on prior knowledge on recommended planting distances under the respective site conditions. For mature, non-irrigated woodlots at average *CWD* (–1293 mm yr$^{-1}$) and of average soil characteristics, increases in stand density lead to pronounced increases in predicted *AGB* until a stand density of approx. 1000 trees ha$^{-1}$; higher densities result in under-proportional further increases in *AGB* (Fig. 4.4b). Our results of increasing stand-scale *AGB* with increasing stand densities up to over 3000 trees ha$^{-1}$ somewhat contrast the results from a previous experimental study on *M. dubia* in South India, which showed slightly higher growth at lower stand densities (below 833 trees ha$^{-1}$) compared to higher stand densities (1000–2500 trees ha$^{-1}$) (Kirankumar and Patil, 2017). However, the study was based on few spatial replicates, the observed differences were not examined statistically and the stands were only four years old at the time of study. Overall, the influence of the stand density of *AGB* growth of *M. dubia* is still associated with too many uncertainties to derive clear management recommendations and requires further experimental studies. Our results do, however, suggest that *M. dubia* can achieve considerable stand-scale growth over a relatively broad range of stand densities, which gives farmers flexibility with regard to producing wood of variable, locally desired dimensions.

**Fig. 4.5.** Fully leafed one-year-old *M. dubia* woodlot with *MAP* over 700 mm (a) and a leaf-shed four-year-old woodlot at *MAP* below 500 mm (b). *M. dubia* logs at an industrial yard for peeling veneers (c) and extracted veneers (d).

The effect of nutrient availability on *AGB* growth was small compared to the effect of water availability (Table 4.1). Our model contained $N_{soil}$ and $P_{soil}$ as predictors for soil nutrient effects, as these are the two macronutrients that are commonly found to limit plant growth (Turner et al., 2018; Soong et al., 2020). $N_{soil}$ varied three-fold across the studied woodlots, and $P_{soil}$ varied fortyfold. While the relatively small positive effect of $N_{soil}$ on *AGB* was non-significant ($p$ = 0.107), the stronger positive effect of $P_{soil}$ was highly significant, indicating partially pronounced soil phosphorus limitations in our study region. Our result of a rather moderate influence of soil nutrient status on *AGBI* is in line with several previous studies on tropical tree species; exceptions are typically only found on severely nutrient-limited sites with drastically reduced growth (Toledo et al., 2011; Alvarez-Clare et al., 2013; Turner et al., 2018; Soong et al., 2020). This is also indicated by the distinctly non-linear effect of $P_{soil}$ on *AGB* of mature, non-irrigated woodlots: while increases in $P_{soil}$ from near zero to approx. 5 mg $kg^{-1}$ result almost in a doubling of *AGB*, further increases in $P_{soil}$ are associated with relatively small increases in *AGB* (Fig. 4.4d). This suggests that there may be room for further growth optimization by informed site selection and by (moderate) fertilizer application on nutrient-poor sites.

## 4.5. Conclusions

We conclude that due to its rapid growth rates in farmland forestry, *M. dubia* is a species with considerable potential for short-rotation plantations in South India and beyond. Its average growth rate across steep environmental and management gradients falls within the range reported for popular tropical tree plantation species. Water availability is the main driver of the growth of *M. dubia*, while the effects of soil nutrients are relatively small. Growth is strongly constrained at sites with high climatological water deficit, but can be increased considerably by irrigation. Generally, there remains large potential for tree-based land use with mixed stands of native species to foster effects of complementarity and optimize ecological benefits

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## 4.7. Appendix: Supplementary materials of Chapter 4.

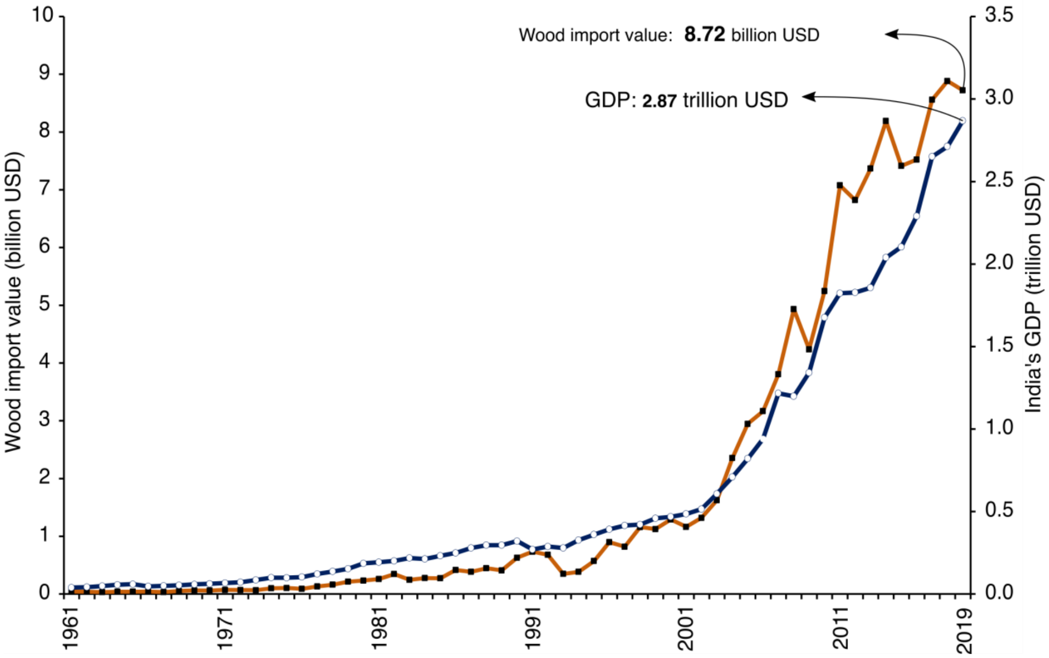


**Fig. 4S1.** India's annual import value of forest products (blank circles with blue line) and gross domestic product (GDP) growth (black squares with orange line), from 1961 to 2019 (FAO, 2021; World Bank, 2021).

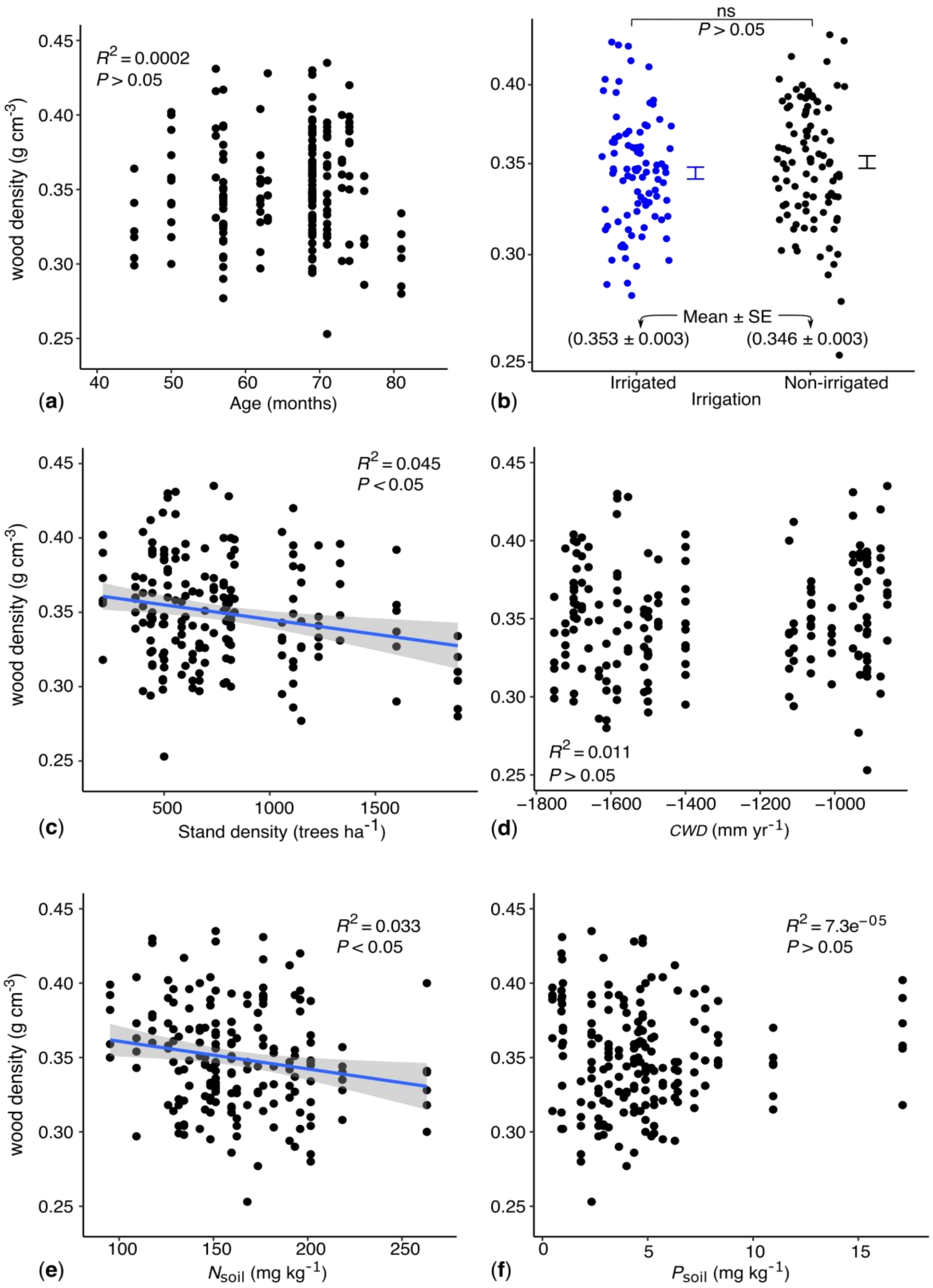


**Fig. 4S2.** The influence of the key variables stands age (**a**), irrigation (**b**), stand density (**c**), climatological water deficit (*CWD*) (**d**), soil nitrogen ($N_{soil}$) (**e**) and soil phosphorus ($P_{soil}$) content (**f**) on wood density. Wood density was measured from cores extracted at breast height on 186 trees across a subset of 31 woodlots. Linear regression models were fitted and regression lines (blue) and standard error corridors (grey) are depicted for $P < 0.05$. The categorical variable irrigation was tested for significant differences ($p < 0.05$) among groups with the Wilcoxon rank sum test (with continuity correction).

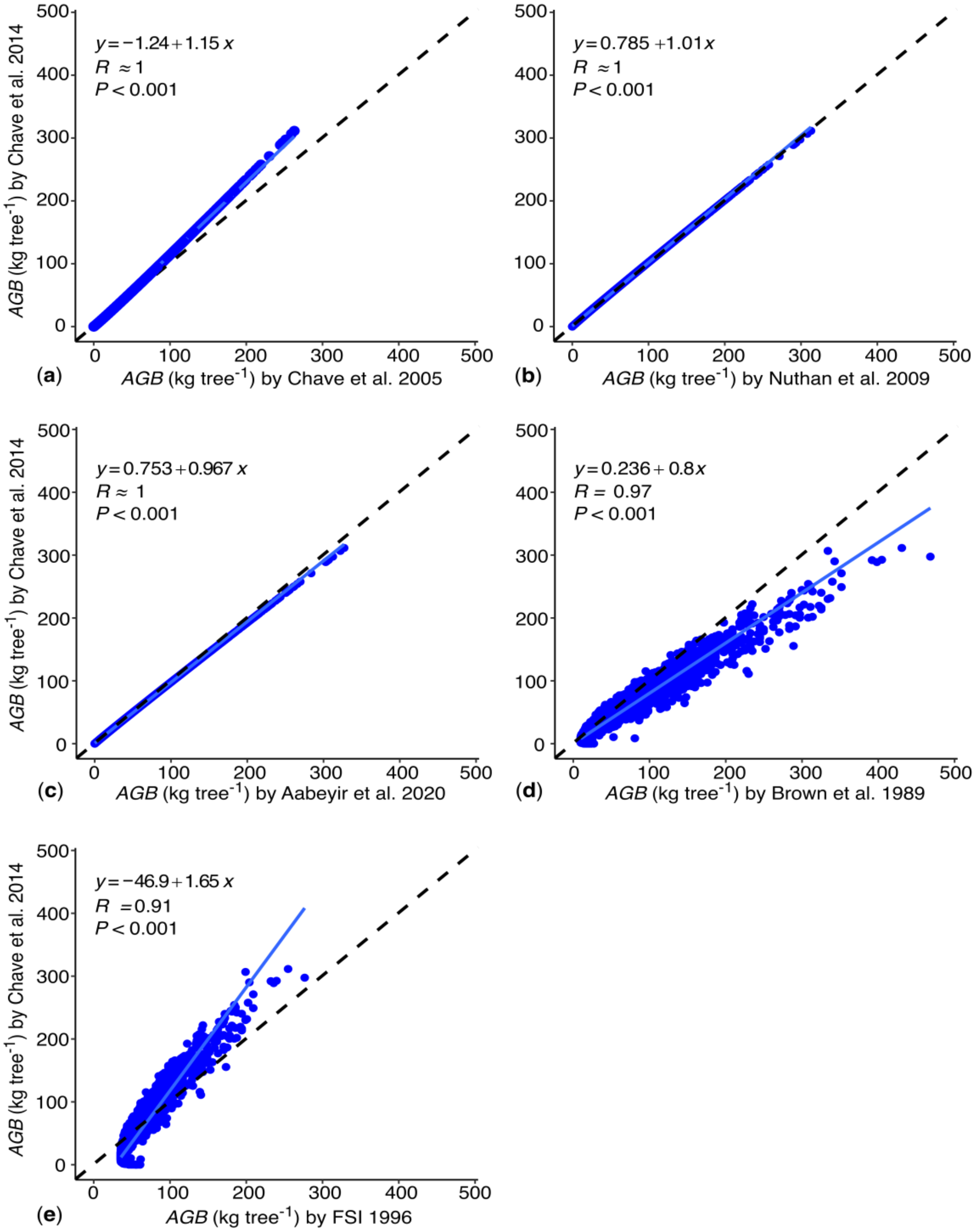
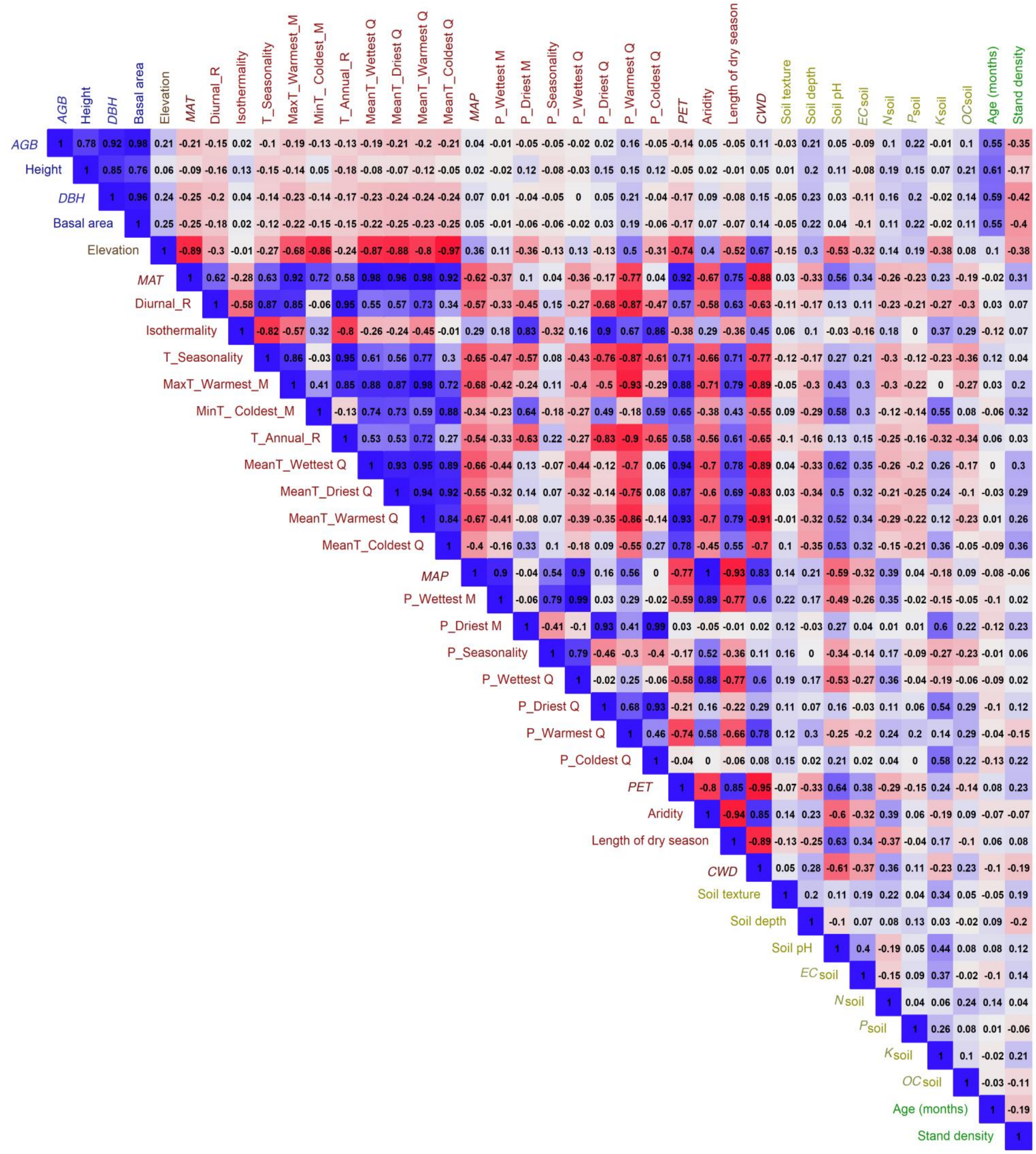


**Fig. 4S3.** Comparison of tree-level aboveground biomass (*AGB*) estimates derived from the pantropical model applied in our study (Chave et al., 2014) to other *AGB* models. Data from all 6,898 studied trees are depicted (dots). The solid blue lines are the respective regression lines, the dashed black lines represent 1:1 line.



| | *AGB* | Height | *DBH* | Basal area | Elevation | *MAT* | Diurnal_R | Isothermality | T_Seasonality | MaxT_Warmest_M | MinT_ Coldest_M | T_Annual_R | MeanT_Wettest Q | MeanT_Driest Q | MeanT_Warmest Q | MeanT_Coldest Q | *MAP* | P_Wettest M | P_Driest M | P_Seasonality | P_Wettest Q | P_Driest Q | P_Warmest Q | P_Coldest Q | *PET* | Aridity | Length of dry season | *CWD* | Soil texture | Soil depth | Soil pH | *EC*soil | *N*soil | *P*soil | *K*soil | *OC*soil | Age (months) | Stand density |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *AGB* | 1 | 0.78 | 0.92 | 0.98 | 0.21 | -0.21 | -0.15 | 0.02 | -0.1 | -0.19 | -0.13 | -0.13 | -0.19 | -0.21 | -0.2 | -0.21 | 0.04 | -0.01 | -0.05 | -0.05 | -0.02 | 0.02 | 0.16 | -0.05 | -0.14 | 0.05 | -0.05 | 0.11 | -0.03 | 0.21 | 0.05 | -0.09 | 0.1 | 0.22 | -0.01 | 0.1 | 0.55 | -0.35 |
| Height | | 1 | 0.85 | 0.76 | 0.06 | -0.09 | -0.16 | 0.13 | -0.15 | -0.14 | 0.05 | -0.18 | -0.08 | -0.07 | -0.12 | -0.05 | 0.02 | -0.02 | 0.12 | -0.08 | -0.03 | 0.15 | 0.15 | 0.12 | -0.05 | 0.02 | -0.01 | 0.05 | 0.01 | 0.2 | 0.11 | -0.08 | 0.19 | 0.15 | 0.07 | 0.21 | 0.61 | -0.17 |
| *DBH* | | | 1 | 0.96 | 0.24 | -0.25 | -0.2 | 0.04 | -0.14 | -0.23 | -0.14 | -0.17 | -0.23 | -0.24 | -0.24 | -0.24 | 0.07 | 0.01 | -0.04 | -0.05 | 0 | 0.05 | 0.21 | -0.04 | -0.17 | 0.09 | -0.08 | 0.15 | -0.05 | 0.23 | 0.03 | -0.11 | 0.16 | 0.2 | -0.02 | 0.14 | 0.59 | -0.42 |
| Basal area | | | | 1 | 0.25 | -0.25 | -0.18 | 0.02 | -0.12 | -0.22 | -0.15 | -0.15 | -0.22 | -0.25 | -0.23 | -0.25 | 0.05 | -0.01 | -0.06 | -0.06 | -0.02 | 0.03 | 0.19 | -0.06 | -0.17 | 0.07 | -0.07 | 0.14 | -0.05 | 0.22 | 0.04 | -0.1 | 0.11 | 0.22 | -0.02 | 0.11 | 0.55 | -0.4 |
| Elevation | | | | | 1 | -0.89 | -0.3 | -0.01 | -0.27 | -0.68 | -0.86 | -0.24 | -0.87 | -0.88 | -0.8 | -0.97 | 0.36 | 0.11 | -0.36 | -0.13 | 0.13 | -0.13 | 0.5 | -0.31 | -0.74 | 0.4 | -0.52 | 0.67 | -0.15 | 0.3 | -0.53 | -0.32 | 0.14 | 0.19 | -0.38 | 0.08 | 0.1 | -0.38 |
| *MAT* | | | | | | 1 | 0.62 | -0.28 | 0.63 | 0.92 | 0.72 | 0.58 | 0.98 | 0.96 | 0.98 | 0.92 | -0.62 | -0.37 | 0.1 | 0.04 | -0.36 | -0.17 | -0.77 | 0.04 | 0.92 | -0.67 | 0.75 | -0.88 | 0.03 | -0.33 | 0.56 | 0.34 | -0.26 | -0.23 | 0.23 | -0.19 | -0.02 | 0.31 |
| Diurnal_R | | | | | | | 1 | -0.58 | 0.87 | 0.85 | -0.06 | 0.95 | 0.55 | 0.57 | 0.73 | 0.34 | -0.57 | -0.33 | -0.45 | 0.15 | -0.27 | -0.68 | -0.87 | -0.47 | 0.57 | -0.58 | 0.63 | -0.63 | -0.11 | -0.17 | 0.13 | 0.11 | -0.23 | -0.21 | -0.27 | -0.3 | 0.03 | 0.07 |
| Isothermality | | | | | | | | 1 | -0.82 | -0.57 | 0.32 | -0.8 | -0.26 | -0.24 | -0.45 | -0.01 | 0.29 | 0.18 | 0.83 | -0.32 | 0.16 | 0.9 | 0.67 | 0.86 | -0.38 | 0.29 | -0.36 | 0.45 | 0.06 | 0.1 | -0.03 | -0.16 | 0.18 | 0 | 0.37 | 0.29 | -0.12 | 0.07 |
| T_Seasonality | | | | | | | | | 1 | 0.86 | -0.03 | 0.95 | 0.61 | 0.56 | 0.77 | 0.3 | -0.65 | -0.47 | -0.57 | 0.08 | -0.43 | -0.76 | -0.87 | -0.61 | 0.71 | -0.66 | 0.71 | -0.77 | -0.12 | -0.17 | 0.27 | 0.21 | -0.3 | -0.12 | -0.23 | -0.36 | 0.12 | 0.04 |
| MaxT_Warmest_M | | | | | | | | | | 1 | 0.41 | 0.85 | 0.88 | 0.87 | 0.98 | 0.72 | -0.68 | -0.42 | -0.24 | 0.11 | -0.4 | -0.5 | -0.93 | -0.29 | 0.88 | -0.71 | 0.79 | -0.89 | -0.05 | -0.3 | 0.43 | 0.3 | -0.3 | -0.22 | 0 | -0.27 | 0.03 | 0.2 |
| MinT_ Coldest_M | | | | | | | | | | | 1 | -0.13 | 0.74 | 0.73 | 0.59 | 0.88 | -0.34 | -0.23 | 0.64 | -0.18 | -0.27 | 0.49 | -0.18 | 0.59 | 0.65 | -0.38 | 0.43 | -0.55 | 0.09 | -0.29 | 0.58 | 0.3 | -0.12 | -0.14 | 0.55 | 0.08 | -0.06 | 0.32 |
| T_Annual_R | | | | | | | | | | | | 1 | 0.53 | 0.53 | 0.72 | 0.27 | -0.54 | -0.33 | -0.63 | 0.22 | -0.27 | -0.83 | -0.9 | -0.65 | 0.58 | -0.56 | 0.61 | -0.65 | -0.1 | -0.16 | 0.13 | 0.15 | -0.25 | -0.16 | -0.32 | -0.34 | 0.06 | 0.03 |
| MeanT_Wettest Q | | | | | | | | | | | | | 1 | 0.93 | 0.95 | 0.89 | -0.66 | -0.44 | 0.13 | -0.07 | -0.44 | -0.12 | -0.7 | 0.06 | 0.94 | -0.7 | 0.78 | -0.89 | 0.04 | -0.33 | 0.62 | 0.35 | -0.26 | -0.2 | 0.26 | -0.17 | 0 | 0.3 |
| MeanT_Driest Q | | | | | | | | | | | | | | 1 | 0.94 | 0.92 | -0.55 | -0.32 | 0.14 | 0.07 | -0.32 | -0.14 | -0.75 | 0.08 | 0.87 | -0.6 | 0.69 | -0.83 | 0.03 | -0.34 | 0.5 | 0.32 | -0.21 | -0.25 | 0.24 | -0.1 | -0.03 | 0.29 |
| MeanT_Warmest Q | | | | | | | | | | | | | | | 1 | 0.84 | -0.67 | -0.41 | -0.08 | 0.07 | -0.39 | -0.35 | -0.86 | -0.14 | 0.93 | -0.7 | 0.79 | -0.91 | -0.01 | -0.32 | 0.52 | 0.34 | -0.29 | -0.22 | 0.12 | -0.23 | 0.01 | 0.26 |
| MeanT_Coldest Q | | | | | | | | | | | | | | | | 1 | -0.4 | -0.16 | 0.33 | 0.1 | -0.18 | 0.09 | -0.55 | 0.27 | 0.78 | -0.45 | 0.55 | -0.7 | 0.1 | -0.35 | 0.53 | 0.32 | -0.15 | -0.21 | 0.36 | -0.05 | -0.09 | 0.36 |
| *MAP* | | | | | | | | | | | | | | | | | 1 | 0.9 | -0.04 | 0.54 | 0.9 | 0.16 | 0.56 | 0 | -0.77 | 1 | -0.93 | 0.83 | 0.14 | 0.21 | -0.59 | -0.32 | 0.39 | 0.04 | -0.18 | 0.09 | -0.08 | -0.06 |
| P_Wettest M | | | | | | | | | | | | | | | | | | 1 | -0.06 | 0.79 | 0.99 | 0.03 | 0.29 | -0.02 | -0.59 | 0.89 | -0.77 | 0.6 | 0.22 | 0.17 | -0.49 | -0.26 | 0.35 | -0.02 | -0.15 | -0.05 | -0.1 | 0.02 |
| P_Driest M | | | | | | | | | | | | | | | | | | | 1 | -0.41 | -0.1 | 0.93 | 0.41 | 0.99 | 0.03 | -0.05 | -0.01 | 0.02 | 0.12 | -0.03 | 0.27 | 0.04 | 0.01 | 0.01 | 0.6 | 0.22 | -0.12 | 0.23 |
| P_Seasonality | | | | | | | | | | | | | | | | | | | | 1 | 0.79 | -0.46 | -0.3 | -0.4 | -0.17 | 0.52 | -0.36 | 0.11 | 0.16 | 0 | -0.34 | -0.14 | 0.17 | -0.09 | -0.27 | -0.23 | -0.01 | 0.06 |
| P_Wettest Q | | | | | | | | | | | | | | | | | | | | | 1 | -0.02 | 0.25 | -0.06 | -0.58 | 0.88 | -0.77 | 0.6 | 0.19 | 0.17 | -0.53 | -0.27 | 0.36 | -0.04 | -0.19 | -0.06 | -0.09 | 0.02 |
| P_Driest Q | | | | | | | | | | | | | | | | | | | | | | 1 | 0.68 | 0.93 | -0.21 | 0.16 | -0.22 | 0.29 | 0.11 | 0.07 | 0.16 | -0.03 | 0.11 | 0.06 | 0.54 | 0.29 | -0.1 | 0.12 |
| P_Warmest Q | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.46 | -0.74 | 0.58 | -0.66 | 0.78 | 0.12 | 0.3 | -0.25 | -0.2 | 0.24 | 0.2 | 0.14 | 0.29 | -0.04 | -0.15 |
| P_Coldest Q | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.04 | 0 | -0.06 | 0.08 | 0.15 | 0.02 | 0.21 | 0.02 | 0.04 | 0 | 0.58 | 0.22 | -0.13 | 0.22 |
| *PET* | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.8 | 0.85 | -0.95 | -0.07 | -0.33 | 0.64 | 0.38 | -0.29 | -0.15 | 0.24 | -0.14 | 0.08 | 0.23 |
| Aridity | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.94 | 0.85 | 0.14 | 0.23 | -0.6 | -0.32 | 0.39 | 0.06 | -0.19 | 0.09 | -0.07 | -0.07 |
| Length of dry season | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.89 | -0.13 | -0.25 | 0.63 | 0.34 | -0.37 | -0.04 | 0.17 | -0.1 | 0.06 | 0.08 |
| *CWD* | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.05 | 0.28 | -0.61 | -0.37 | 0.36 | 0.11 | -0.23 | 0.23 | -0.1 | -0.19 |
| Soil texture | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.2 | 0.11 | 0.19 | 0.22 | 0.04 | 0.34 | 0.05 | -0.05 | 0.19 |
| Soil depth | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.1 | 0.07 | 0.08 | 0.13 | 0.03 | -0.02 | 0.09 | -0.2 |
| Soil pH | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.4 | -0.19 | 0.05 | 0.44 | 0.08 | 0.08 | 0.12 |
| *EC*soil | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.15 | 0.09 | 0.37 | -0.02 | -0.1 | 0.14 |
| *N*soil | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.04 | 0.06 | 0.24 | 0.14 | 0.04 |
| *P*soil | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.26 | 0.08 | 0.01 | -0.06 |
| *K*soil | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.1 | -0.02 | 0.21 |
| *OC*soil | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.03 | -0.11 |
| Age (months) | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.19 |
| Stand density | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |

**Fig. 4S4.** Correlation matrix of available growth, climate, soil and management variables. Units and descriptions for all variables are presented in Table 4S1

**Table 4S1**. List of available growth, climate, soil and management variables. Given are the measurement units, means, standard deviations, standard errors, minimum and maximum values among the 186 studied woodlots.

| S# | Variables | Unit | Mean | SD | SE | Minimum | Maximum |
|---|---|---|---|---|---|---|---|
| 1 | Aboveground biomass (*AGB* ) at plot level | Mg ha$^{-1}$ | 29.63 | 25.28 | 1.85 | 0.29 | 110.36 |
| 2 | Mean monthly *AGBI* | Mg ha$^{-1}$ month$^{-1}$ | 0.73 | 0.55 | 0.04 | 0.03 | 2.75 |
| 3 | Average annual *AGBI* | Mg ha$^{-1}$ year$^{-1}$ | 8.76 | 6.64 | 0.49 | 0.42 | 32.95 |
| 4 | Height | m | 9.46 | 3.53 | 0.26 | 1.48 | 17.58 |
| 5 | *DBH* | cm | 12 | 5.13 | 0.38 | 2.53 | 26.46 |
| 6 | Basal area | m$^{2}$ ha$^{-1}$ | 10.2 | 6.51 | 0.48 | 0.03 | 27.59 |
| 7 | Altitude | m | 675.46 | 157.9 | 11.6 | 328 | 951 |
| 8 | Age | month | 39.05 | 22.06 | 1.62 | 6 | 113 |
| 9 | Age | Year | 3.25 | 1.84 | 0.14 | 0.5 | 9.42 |
| 10 | Stand density | Trees ha$^{-1}$ | 905.54 | 555.9 | 40.8 | 116 | 3086 |
| 11 | Irrigation[a] | Category | -- | -- | -- | -- | -- |
| 12 | Mean Annual Temperature (*MAT* ) | °C | 24.95 | 1.42 | 0.1 | 22.5 | 27.4 |
| 13 | Mean Diurnal Range (Mean of monthly (max T - min T)) | °C | 10.26 | 0.87 | 0.06 | 8.8 | 11.3 |
| 14 | Isothermality (BIO2/BIO7) (* 100) | % | 0.57 | 0.02 | 0 | 0.53 | 0.62 |
| 15 | Temperature Seasonality (standard deviation *100) | % | 187.68 | 32.51 | 2.38 | 142.2 | 247.3 |
| 16 | Max Temperature of Warmest Month | °C | 34.57 | 2.19 | 0.16 | 31 | 37.8 |
| 17 | Min Temperature of Coldest Month | °C | 16.56 | 1.05 | 0.08 | 14.6 | 19.4 |
| 18 | Temperature Annual Range (BIO5-BIO6) | °C | 18.02 | 1.97 | 0.14 | 14.9 | 20.4 |
| 19 | Mean Temperature of Wettest Quarter | °C | 24.54 | 1.24 | 0.09 | 21.7 | 27 |
| 20 | Mean Temperature of Driest Quarter | °C | 24.65 | 1.44 | 0.11 | 21.8 | 26.7 |
| 21 | Mean Temperature of Warmest Quarter | °C | 27.74 | 1.7 | 0.12 | 24.9 | 30.5 |
| 22 | Mean Temperature of Coldest Quarter | °C | 22.77 | 1.06 | 0.08 | 21.1 | 24.9 |
| 23 | Mean Annual Precipitation (*MAP* ) | mm | 874.94 | 351.2 | 25.8 | 421 | 2171 |
| 24 | Precipitation of Wettest Month | mm | 206.73 | 119 | 8.73 | 102 | 804 |
| 25 | Precipitation of Driest Month | mm | 1.48 | 2.39 | 0.18 | 0 | 9 |
| 26 | Precipitation Seasonality (Coefficient of Variation) | % | 0.9 | 0.11 | 0.01 | 0.78 | 1.42 |
| 27 | Precipitation of Wettest Quarter | mm | 436.69 | 210.3 | 15.4 | 227 | 1537 |
| 28 | Precipitation of Driest Quarter | mm | 10.62 | 9.31 | 0.68 | 1 | 34 |
| 29 | Precipitation of Warmest Quarter | mm | 151.83 | 58.18 | 4.27 | 74 | 263 |
| 30 | Precipitation of Coldest Quarter | mm | 57.48 | 36.97 | 2.71 | 19 | 169 |
| 31 | Potential Evapotranspiration (*PET* ) | mm | 1991.7 | 129.5 | 9.49 | 1786 | 2289 |
| 32 | Aridity Index (annual) | -- | 0.45 | 0.2 | 0.01 | 0.19 | 1.19 |
| 33 | Length of dry season | month | 10.26 | 1.43 | 0.1 | 7 | 12 |
| 34 | Aridity Index in dry months | -- | 0.3 | 0.05 | 0 | 0.15 | 0.48 |
| 35 | Climatological water deficit (*CWD* ) | mm yr$^{-1}$ | -1293 | 266.8 | 19.6 | -1844 | -824 |
| 36 | Soil depth | cm | 74.08 | 27.27 | 2 | 30.48 | 152.4 |
| 37 | Soil texture[a] | Class | -- | -- | -- | -- | -- |
| 38 | Soil pH | -- | -- | -- | -- | 4.32 | 8.8 |
| 39 | $EC_{soil}$ (electrical conductivity) | dS m$^{-1}$ | 1.41 | 1.41 | 0.1 | 0.19 | 9.23 |
| 40 | $N_{soil}$ (nitrogen content) | mg kg$^{-1}$ | 155.64 | 35.96 | 2.64 | 75.6 | 266 |
| 41 | $P_{soil}$ (phosphorous content) | mg kg$^{-1}$ | 4 | 3.5 | 0.3 | 0.4 | 17.3 |
| 42 | $K_{soil}$ (potassium content) | mg kg$^{-1}$ | 31.9 | 21.1 | 1.6 | 7.6 | 130.5 |
| 43 | $OC_{soil}$ (organic carbon content) | % by mass | 0.5 | 0.21 | 0.02 | -0.21 | 0.87 |

*AGBI*: Aboveground biomass increment; [a] categorical variable: irrigated vs. non-irrigated; soil texture class (sand, silt, clay).

**Table 4S2**. Aboveground biomass (*AGB*), average annual *AGB* increment (*AGBI*), key characteristics (age, stand density, mean annual precipitation *MAP*, soil conditions) and further information on tropical tree plantations as cited for comparison to our study.

| **Species** | **Country** | **Age (year)** | **Plots or Replicates** | **Stand density (trees ha$^{-1}$)** | ***AGB* (Mg ha$^{-1}$)** | ***AGBI* (Mg ha$^{-1}$ yr$^{-1}$)** | ***MAP* (mm yr$^{-1}$)** | **Soil conditions** | ***AGB* estimation method** | **Reference** |
|---|---|---|---|---|---|---|---|---|---|---|
| *Melia dubia* | South India | 9 | 186 | 905 ± 41 (Mean ± SE) | 93.77$^{A}$ | 10.41$^{A}$ | 420-2170 | Diverse | Chave et al. (2014) | Present study |
| | India (Karnataka)$^{\#}$ | 4 | 3 | 2500 | 47.68 | 11.22 | 880 | Black cotton soil | *AGB* estimates were derived in analogy to our study using *DBH* and height | Kirankumar and Patil, 2017 |
| | | | 3 | 1666 | 40.58 | 9.55 | | | | |
| | | | 3 | 1250 | 47.89 | 11.27 | | | | |
| | | | 3 | 1000 | 45.83 | 10.78 | | | | |
| | | | 3 | 833 | 54.16 | 12.74 | | | | |
| | | | 3 | 714 | 50.98 | 12.00 | | | | |
| | | | 3 | 625 | 40.90 | 9.62 | | | | |
| *Acacia auriculiformis* | India (Kerala) | 8.8 | 3 | 1250 | 326.43 | 37.09 | 2569 | Acidic oxisols | Harvest-calculated | Kumar et al., 1998 |
| *Acacia melanoxylon* | Chile | 4 | 3 | 5000 | 2.60 | 0.65 | 1102 | Sandy soils | Harvest-measured allometric | Acuña et al., 2017 |
| | | | 3 | 5000 | 9.60 | 2.40 | 695 | Dry, granitic soils | | |
| *Ailanthus triphysa* | India (Kerala) | 8.8 | 3 | 1250 | 40.54 | 4.61 | 2569 | Acidic oxisols | Harvest-calculated | Kumar et al., 1998 |
| *Albizia procera* | Puerto Rico | 5.5 | 6 | 2500 | 124.00 | 22.55 | 1100 | Fraternidad clay | Harvest-calculated | Wang et al., 1991 |
| *Casuarina equisetifolia* | India (Tamil Nadu) | 2 | 3 | 6666 | 75.04 | 37.52 | 450-650 | Sandy clay loam | Harvest-calculated | Rajendran and Devaraj, 2004 |
| | Puerto Rico | 5.5 | 6 | 2500 | 199.00 | 36.18 | 1100 | Fraternidad Clay | Harvest-calculated | Wang et al., 1991 |
| | India (Uttar Pradesh) | 7 | 3 | 2500 | 205.10 | 29.30 | 1000 | Silty clay loam, sodic soil | Harvest-calculated | Rana et al., 2001 |
| | | | 3 | 2500 | 134.70 | 19.24 | | | | |
| | | | 3 | 2500 | 176.60 | 25.23 | | | | |
| | India (Kerala) | 8.8 | 3 | 1250 | 95.58 | 10.86 | 2569 | Acidic oxisols | Harvest-calculated | Kumar et al., 1998 |
| *Dalbergia sissoo* | India (Karnataka) | 3 | 24 | 2500 | 7.60 | 2.53 | 800 | Deep lateritic | Harvest-calculated | Hunter 2001 |
| | India (Uttar Pradesh) | 6 | 3 | 1967 | 16.29 | 2.71 | 977 | Sodic soil | Harvest-measured allometric | Tyagi et al., 2009 |
| | | 9 | 3 | 1600 | 38.31 | 4.26 | | | | |
| *Dalbergia sissoo* | India (Uttarakhand) | 10 | 3 | 1666 | 77.90 | 7.79 | 1364 | Sandy loam | Harvest-calculated | Kanime et al., 2013 |
| *Gmelina arborea* | Nigeria | 7 | 12 | 1736 | 85.6 | 12.2 | 1125 | NA | Harvest-calculated | Fuwape and Akindele, 1997 |
| | India (Chhattisgarh) | 4 | 5 | 2500 | 8.99 | 2.25 | 1250 | Black deep clay | Harvest-calculated | Swamy et al., 2003a |
| | | | 5 | 1750 | 3.88 | 0.97 | | | | |
| | | | 5 | 1250 | 2.87 | 0.72 | | | | |
| | | | 5 | 1000 | 2.19 | 0.55 | | | | |
| | India (Chhattisgarh) | 6 | 5 | 737 | 41.12 | 6.85 | 1200 | Red lateritic soil | Harvest-measured allometric | Swamy et al., 2003b |
| | | | 5 | 724 | 39.30 | 6.55 | | | | |
| | | | 5 | 740 | 51.20 | 8.53 | | | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *E. camadulensis* | Chile | 4 | 3 | 5000 | 14.90 | 3.73 | 695 | Dry, granitic soils | Harvest-measured allometric | Acuña et al., 2017 |
| *E. globulus* | Chile | | 3 | 5000 | 22.50 | 5.63 | 1102 | Sandy soils | | |
| *Eucalyptus nitens* | Chile | 4 | 3 | 5000 | 23.40 | 5.85 | 1048 | Sandy soils | Harvest- allometric | Acuña et al., 2017 |
| | | | 3 | | 14.60 | 3.65 | 695 | Dry, granitic soils | | |
| *Eucalyptus regnans* | New Zealand | 4 | 1 | 2050 | 68.5 | 17.12 | 1489$^{A}$ | Sandy loam | Harvest-calculated | Frederick et al., 1985a |
| | | 7 | 1 | 1850 | 198.00 | 28.29 | | | | |
| | | 17 | 1 | 1250 | 460.00 | 27.06 | | | | |
| *Eucalyptus robusta* | Puerto Rico | 5.5 | 6 | 2500 | 67.00 | 12.18 | 1100 | Fraternidad Clay | Harvest-calculated | Wang et al., 1991 |
| *Eucalyptus saligna* | New Zealand | 8 | 1 | 829 | 129.8 | 16.22 | 1662 $^{B}$ | OropiKaharoa | Harvest-calculated | Frederick et al., 1985b |
| *E. tereticornis* | India (Tamil Nadu) | 7 | 4 trees | 1060 | 95.17 | 13.60 | 916 | Sandy loam | NA | Negi and Sharma, 1985 |
| | India (Uttarakhand) | 10 | NA | 992 | 126.1 | 12.61 | 1727 | Alluvial and clay | NA | Rawat and Negi, 2004 |
| | India (Haryana) | 10 | 1 | 6530 | 122.5 | 12.25 | 766 | Silt-loam on improved sodic land | Harvest-calculated | Minhas et al., 2015 |
| | | | 1 | 1993 | 261.5 | 26.15 | | | | |
| | | | 1 | 517 | 177.5 | 17.75 | | | | |
| | | | 1 | 163 | 54.6 | 5.46 | | | | |
| (Boundary plantation) | India (Uttarakhand) | 10 | | 120 | 21.22 | 2.12 | 1364 | Sandy loam | Harvest-calculated | Kanime et al., 2013 |
| *Leucaena leucocephala (var. K8)* | Puerto Rico | 5.5 | 6 | 2500 | 47.00 | 8.55 | 1100 | Fraternidad Clay | Harvest-calculated | Wang et al., 1991 |
| *var.P.R.* | | 5.5 | 6 | 2500 | 33.00 | 6.00 | 1100 | | | |
| | India (Kerala) | 8.8 | 3 | 1250 | 22.81 | 2.59 | 2569 | Acidic oxisols | Harvest-calculated | Kumar et al., 1998 |
| *Populus deltoides* | India (Uttarakhand) | 1 | 3 | 500 | 1.26 | 1.26 | 1364 | Sandy clay loam | Harvest-calculated | Arora et al., 2014 |
| | | 5 | 3 | 500 | 52.95 | 10.59 | | | | |
| | | 11 | 3 | 500 | 180.24 | 16.39 | | | | |
| | India (Uttarakhand) | 8 | 3 | 500 | 50.10 | 6.26 | 1364 | Sandy loam | Harvest-calculated | Kanime et al., 2013 |
| *Pterocarpus marsupium* | India (Kerala) | 8.8 | 3 | 1250 | 66.11 | 7.51 | 2569 | Acidic oxisols | Harvest-calculated | Kumar et al., 1998 |
| *Tectona grandis* | India (Uttar Pradesh) | 4 | 10 trees | 3490 | 25.40 | 6.35 | 900 | Sandy loam | Harvest-calculated | Baishya et al., 2009 |
| | | 14 | 14 trees | 1040 | 39.92 | 2.85 | 900 | | | Karmacharya & Singh, 1992 |
| | | 30 | 10 trees | 474 | 76.95 | 2.57 | 900 | | | |
| | India (Tamil Nadu) | 20 | NA | NA | 320.00 | 16.00 | 1100 | NA | Harvest-measured allometric | Buvaneswaran et al., 2006 |
| | | 47 | NA | NA | 410.00 | 8.72 | 1100 | NA | | |

[#]Mean tree diameter and height were used with a wood density of 0.35 g $cm^{-3}$; [A]model-estimated average *AGB* for nine-year-old *M. dubia* plantations as presented in our study; [B] precipitation (mm) was extracted from WorldClim database (Version 2, http://worldclim.org); NA: no data available.

# Chapter 5: Variability in growth-determining hydraulic wood and leaf traits in *Melia dubia* across a steep water availability gradient in southern India

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# 5. Variability in growth-determining hydraulic wood and leaf traits in *Melia dubia* across a steep water availability gradient in southern India

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## Abstract

In India, short-rotation plantations have increasingly been promoted over the last decades in response to altered forest management policy and increased wood demand. Understanding how short-rotation forest species coordinate fast growth with water demand and carbon investment will help improving management decisions.

We investigated the intra-specific variability in growth performance, leaf traits, and wood anatomical and derived hydraulic properties in 31 *Melia dubia* (Meliaceae) plantations along a steep rainfall gradient from 450 to 1,700 mm $yr^{-1}$, and addressed the role of different irrigation practices and soil nutrient availability.

We found water supply and soil nutrient status to have a dominant influence on the aboveground biomass increment (*AGBI*) of *M. dubia*. *AGBI* was higher at irrigated sites with a less negative climatological water balance (i.e. with lower rainfall) and at sites with higher soil phosphorus availability. Stem wood anatomical traits associated with the water transport capacity mirrored the patterns in *AGBI*. At sites with higher water and soil phosphorus availability, the xylem was composed of larger vessel diameters and lower vessel densities. However, both branch wood anatomical traits and leaf traits including the leaf-to-sapwood area ratio were largely independent of water availability and soil conditions.

We conclude that a high stem hydraulic efficiency determined by large xylem vessels is a prerequisite for high aboveground productivity, and that the growth of *M. dubia* may often be phosphorus-limited. Short-rotation plantations with *M. dubia* will therefore clearly benefits from continuous irrigation in regions that receive annual precipitations substantially below 1,000 mm $yr^{-1}$. This highlights the potential to increase yields in this important short-rotation forest species by improving irrigation and fertilization protocols.

**Keywords:** Aboveground biomass, Huber value, Hydraulic conductivity, Leaf morphology, Precipitation gradient, Productivity, Wood anatomy

## 5.1. Introduction

Globally, the demand for fuelwood and industrial roundwood has increased since the 1960s, a trend which is expected to continue (Buongiorno et al., 2011). In India, for example, the import value of wood and wood products increased from 0.04 billion USD in 1961 to 8.7 billion USD in 2019 (FAO, 2021). Prevailing forest policy and economic reforms are expected to create additional demand for wood and severe shortage of domestic supply in the future (Ghosh and Sinha, 2016; Shrivastava and Saxena, 2017). To reduce the pressure on forests, short rotation plantations with native and exotic tree species are being promoted throughout the country (MoA, 2014; Ghosh and Sinha, 2019). In India, the estimated annual wood production from agroforestry, farm forestry and trees grown outside forests was 42 million cubic meters in the year 2011 (FSI, 2011). A growing number of studies have investigated the potential negative impacts of some commonly used exotic species on soil, water and biodiversity (Rangan et al., 2010; Bilal et al., 2014; Zhou et al., 2020). In light of potential adverse effects of exotic species and the goal to widen the spectrum of cultivated tree species, planting native tree species has been encouraged in the recent years (Amazonas et al., 2018; Liu et al., 2018; Castro-Díez et al., 2019; Zhou et al., 2020).

In India, *Melia dubia* Cav. is emerging as a promising native tree species for short-rotation plantations for the plywood, paper and engineered-wood industries (Parthiban et al., 2009; Sinha et al., 2019; Thakur et al., 2018, 2020). The species yields termite and fungus resistant high-quality timber (Suprapti et al., 2007), suitable for furniture, agricultural implements and construction purposes (Mandang and Artistien, 2003). It is also suitable for producing medicine, firewood and fodder (Nagalakshmi et al., 2003; Vijayan et al., 2004; Parthiban et al., 2009). *M. dubia*, commonly known as Malabar neem or Burma neem, is a drought-deciduous species that naturally occurs in moist deciduous forests on the Indian subcontinent, and is indigenous to the Western Ghats of India (Thakur et al., 2020). It is cultivated across large climatic and soil moisture gradients throughout India and in Southeast Asia (Nguyen et al., 2016; Rambey et al., 2019), as block plantations or in agroforestry systems (Thakur et al., 2018). Its cultivation has expanded in recent decades because of its economic value and fast growth. The global distributional range of the species has been extended to Sri Lanka, Malaysia, Indonesia, China and Australia (Saravanan et al., 2013). The native range of the species extends from humid lowlands to plateaus at up to 1,800 m a.s.l. elevation in the Eastern Himalayas (Nguyen et al., 2016), covering moist deciduous to dry deciduous tropical forests.

Plant productivity is known to scale with water availability (Wright et al., 2001; Guan et al., 2015; Berner et al., 2017) and the water transport capacity of the xylem (Poorter et al., 2010; Hoeber et al., 2014; Kotowska et al., 2021). Plants can achieve higher xylem conductivity by producing wider vessels, as according to the Hagen-Poiseuille equation the conductivity of a vessel scales with the fourth power of its diameter. The classic principle of plant hydraulic architecture postulates that the wood of trees growing in dry environments is composed of smaller xylem conduits than the wood of trees from wet environments (Carlquist, 1977; Chenlemuge et al., 2015; Pfautsch et al., 2016). According to our most recent understanding, water limitation does not *per se* result in the formation of smaller xylem conduits, but does affect the growth rate and tree height (Lechthaler et al., 2019; Fajardo et al., 2020). Because the flow path length, i.e. the distance from the apex towards the stem base, strongly affects vessel dimensions at the stem base (Olson et al., 2021), many previous reports of differing vessel dimensions across sites might simply reflect different tree heights. Hence, recent studies have emphasized the role of tree size (particularly distance from the apex to the stem base) and cambial age for the comparability and interpretation of hydraulic-climate relationships (Rosell et al., 2017; Li et al., 2019; Soriano et al., 2020), highlighting the need to compare branches of similar size and from a similar canopy position to reduce the influence of vertical or radial gradients when studying trees exposed to different environmental conditions (cf. Petit et al., 2016).

Xylem hydraulic properties are expected to be coordinated with leaf functional traits (Brodribb, 2009). A high hydraulic efficiency has been found to be essential to maintain high transpiration and carbon gain rates per unit leaf area (Zhang et al., 2016). Further, a high specific leaf area (*SLA*) has been associated with low carbon investment per wood volume (Poorter et al., 2010), while leaf-to-sapwood area ratios are linked to a habitat's hydroclimate (Martinez-Vilalta et al., 2009; Gleasonet al., 2016; Anderegg et al., 2021). Thereby, intraspecific adjustments along water availability gradients rely on changes in resource allocation between sapwood and leaf area (Mencuccini et al., 2019; Rosas et al., 2019).

In order to increase yield in drought-prone environments, it has been recommended to irrigate forest plantations (Armitage, 1985). So far, the influence of irrigation on tree hydraulics traits is less well-explored than vascular adjustments along natural water availability gradients. Studies on current year branches of seasonally irrigated olive trees (Torres-Ruiz et al., 2013) and young willows (Achinelli et al., 2018), however, reported no marked variation in conduit diameter and density, potentially because the flow path length was unaffected. Along with irrigation, nutrient availability also enhances tree productivity (Stape et al., 2010; Campoe et al., 2013; P´erez-Cruzado et al., 2014). The increased availability of nutrients positively impacts average vessel diameter, resulting in higher specific conductivity and increased growth rates (Hacke et al., 2017). Nonetheless, tree hydraulic research frameworks dealing with responses to drought have largely focused on water and carbon associated mechanisms, whereas the role of nutrients is often overlooked (Gessler et al., 2017). Indeed, semi-arid tropical regions tend to have low soil fertility (Wani et al., 2011) while humid tropical lowland ecosystems are relatively rich in available $N_{\mathrm{soil}}$ (Vitousek, 1984; Sollins, 1998) and growth rate is likely to be limited by $P_{\mathrm{soil}}$ or other rock-derived nutrients (Tanner et al., 1998).

Despite the increasing popularity of *M. dubia* in farm and agroforestry and its extensive distribution across hydroclimatic regimes, to our knowledge studies related to its hydraulic architecture so far are missing. Given the importance of an efficient hydraulic system for plant biomass accumulation (cf. Tyree, 2003; Brodribb, 2009), it is important to understand the variability of the hydraulic architecture of *M. dubia* across a wide range of environmental conditions. In this study, we collected stem and branch samples from 186 trees belonging to 31 irrigated and non-irrigated sites across a steep climatic gradient in southern India to analyze the potential effect of water and soil nutrient availability on wood anatomical and derived hydraulic traits as well as leaf morphological adjustments in *M. dubia*. We hypothesize that i) reduced water and nutrient availability lead to lower aboveground biomass increment, which is mirrored in ii) smaller xylem vessels and thus lower hydraulic efficiency in similar-sized stems, iii) a decline in the leaf-to-sapwood area ratio driven by the formation of smaller and thicker leaves and iv) more frequent stomatal closure, which is reflected in less negative carbon isotope signatures.

## 5.2. Materials and methods

### *5.2.1. Study sites*

We selected 31 out of 186 plantations that were studied for biomass production in a companion study across a rainfall gradient in South India (Röll et al., 2021). In each plantation, plots of 20 m × 20 m were established in 2017. The selected subset of plots ranged from 45 to 81 months in age and covered a steep rainfall gradient from 450 to 1,700 mm $yr^{-1}$. The region experiences a seasonal tropical climate with significant intra-seasonal variability in rainfall and a pronounced dry season. Plots with a mean annual precipitation (*MAP*) below 1,000 mm $yr^{-1}$ were classified as dry plots and plots with a *MAP* equal to or larger than 1,000 mm $yr^{-1}$ were classified as wet plots (Fig. 5.1). The mean annual temperature (*MAT*) ranged from 25.4 to 27.6 °C at dry sites and 22.9 to 24.1 °C at wet sites (Karger et al., 2017). According to the aridity index by Trabucco and Zomer (2019), the dry and wet plots represented semiarid (0.26) and dry sub-humid (0.59) climate class with average evapotranspiration of 2,151 mm $yr^{-1}$ and 1,860 mm $yr^{-1}$, respectively. All woodlots were irrigated in the initial year after their establishment to avoid loss of the seedlings. In the majority (66%) of the sites, irrigation continued over the entire rotational cycle with a reduced frequency, while the remaining sites were kept in an exclusively rainfed watering scheme. In the following, the plots in which trees were watered only during the establishment season are referred as “non-irrigated”, while the plots watered during successive dry seasons are referred to as “irrigated”. A list of acronyms used in the study is provided in Table 5.1, while the average environmental conditions and stand characteristics of the stands are summarized in Table 5.2.

### *5.2.2. Environmental variables*

We extracted bioclimatic variables for the location of each woodlot from the CHELSA database (Version 1.2, http://chelsa-climate.org, Karger et al., 2017) using the R packages raster (Hijmans, 2020) and sp (Bivand et al., 2013). The data are provided as monthly averages for the years 1979–2013 at a spatial resolution of 30 arc seconds. Further, monthly potential evapotranspiration (*ET*0, mm) and annual aridity index were extracted from Climate Database (Version 3, https://cgiarcsi.community) developed by Trabucco and Zomer, (2019). The climatological water deficit (*CWD*, mm $yr^{-1}$) was calculated by summing up the difference between monthly *MAP* and potential evapotranspiration (*PET*) for all months having negative rainfall balance according to Chave et al. (2014) and was used as a proxy for water stress. We further approximated the number of wet months per year following Walter and Lieth's (1967) classical approach as the number of months during which precipitation in mm exceeded twice the average temperature in °C.

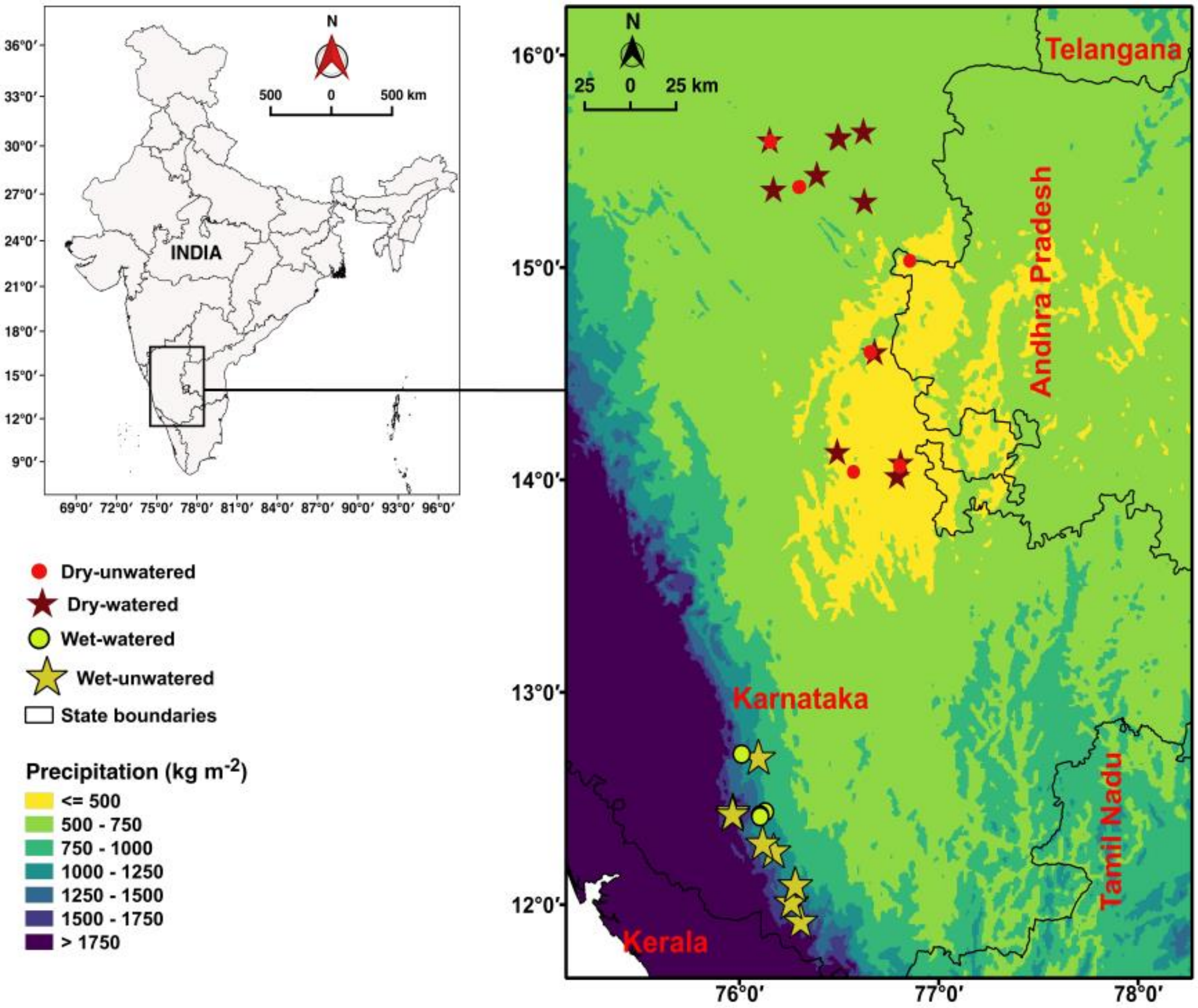

**Fig. 5.1.** Study area and location of the 31 woodlots. The sites span across a gradient in mean annual precipitation ranging from 452 to 1,696 mm $yr^{-1}$.

The soil properties were estimated from a composite soil sample collected at 15 cm soil depth from five different locations in each plot. The soil organic carbon content ($OC_{\mathrm{soil}}$, % mass) was estimated by the rapid titration method. In addition, available soil nitrogen ($N_{\mathrm{soil}}$, mg kg$^{-1}$), soil phosphorus ($P_{\mathrm{soil}}$, mg kg$^{-1}$) and soil potassium ($K_{\mathrm{soil}}$, mg kg$^{-1}$) were analyzed.

**Table 5.1.** List of variables included in the study with definitions and units.

| Variable | Unit | Expansion/explanation |
|---|---|---|
| $DBH$ | cm | Diameter at breast height (at 1.3 m) |
| $H$ | m | Tree height |
| Age | yr | Stand/ tree age |
| $WD$ | g cm$^{-3}$ | Wood density |
| $AGB$ | kg | Tree aboveground biomass |
| $AGBI$ | kg yr$^{-1}$ | Aboveground biomass increment |
| Stem $D$ | µm | Average stem vessel diameter |
| Stem $VD$ | n mm$^{-2}$ | Stem vessel density |
| Stem $D_{\mathrm{h}}$ | µm | Stem hydraulically-weighted vessel diameter |
| Stem $K_{\mathrm{p}}$ | kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$ | Stem potential hydraulic conductivity |
| Branch $D$ | µm | Average branch vessel diameter |
| Branch $VD$ | n mm$^{-2}$ | Branch vessel density |
| Branch $D_{\mathrm{h}}$ | µm | Branch hydraulically-weighted vessel diameter |
| Branch $K_{\mathrm{p}}$ | kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$ | Branch potential hydraulic conductivity |
| $K_{\mathrm{l}}$ | $10^{-4}$ kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$ | Branch theoretical leaf-specific conductivity |
| $A_{\mathrm{leaf}}$ | cm$^{2}$ | Mean leaf area |
| $A_{\mathrm{l}}$: $A_{\mathrm{s}}$ | m$^{2}$ cm$^{-2}$ | Leaf-to-sapwood area ratio |
| $SLA$ | cm$^{2}$ g$^{-1}$ | Specific leaf area |
| $\delta^{13}$C | ‰ | Carbon isotopic signature |
| Altitude | m a.s.l. | Altitude, above sea level |
| $MAP$ | kg m$^{-2}$ | Mean annual precipitation |
| $MAT$ | °C | Mean annual temperature |
| $ET_{0}$ | mm yr$^{-1}$ | Evapotranspiration |
| $AI\text{-}ET_{0}$ | | Aridity index |
| $CWD$ | mm yr$^{-1}$ | Climatological water deficit |
| No. wet months | n yr$^{-1}$ | Number of wet months in a year |
| $N_{\mathrm{soil}}$ | mg kg$^{-1}$ | Available soil nitrogen |
| $P_{\mathrm{soil}}$ | mg kg$^{-1}$ | Available soil phosphorous |
| $K_{\mathrm{soil}}$ | mg kg$^{-1}$ | Available soil potassium level |
| $OC_{\mathrm{soil}}$ | % by mass | Soil organic content |

**Table 5.2.** Stand structural and environmental characteristics. Given are the means ± SE for wet and dry regions, separated between irrigated and non-irrigated sites. Letters indicate significant differences in pairwise t-tests with Tukey's correction for multiple comparisons on a $p < 0.05$ significance level. For acronyms, see Table 5.1.

| Variables | Unit | Wet (>1000 mm *MAP*) | | Dry (< 700 mm *MAP*) | |
|---|---|---|---|---|---|
| | | Irrigated | Non-irrigated | Irrigated | Non-irrigated |
| Number of plots | | 4 | 9 | 11 | 7 |
| Number of trees | | 24 | 54 | 66 | 42 |
| *H* | m | $15.57 \pm 0.26^{b}$ | $14.49 \pm 0.33^{b}$ | $14.76 \pm 0.26^{b}$ | $10.87 \pm 0.33^{a}$ |
| *DBH* | cm | $22.33 \pm 0.87^{c}$ | $19.35 \pm 0.33^{b}$ | $19.72 \pm 0.56^{b}$ | $14.41 \pm 0.53^{a}$ |
| *WD* | g cm$^{-3}$ | $0.344 \pm 0.005^{a}$ | $0.357 \pm 0.005^{a}$ | $0.347 \pm 0.004^{a}$ | $0.347 \pm 0.005^{a}$ |
| *AGB* | kg | $159.21 \pm 14.35^{c}$ | $109.73 \pm 5.04^{b}$ | $121.4 \pm 7.6^{b}$ | $49.55 \pm 4.48^{a}$ |
| Age | yr | $5.35 \pm 0.09^{a}$ | $5.33 \pm 0.1^{a}$ | $5.58 \pm 0.08^{a}$ | $5.43 \pm 0.13^{a}$ |
| Altitude | m.a.s.l | $905.00 \pm 3.81^{b}$ | $817.33 \pm 8.93^{b}$ | $540.91 \pm 9.43^{a}$ | $562.29 \pm 8.33^{a}$ |
| *MAT* | °C | $23.08 \pm 0.02^{a}$ | $23.57 \pm 0.05^{a}$ | $26.67 \pm 0.08^{b}$ | $26.46 \pm 0.07^{b}$ |
| *MAP* | mm yr$^{-1}$ | $1167.25 \pm 12.80^{b}$ | $1333.67 \pm 28.59^{b}$ | $547.55 \pm 8.35^{a}$ | $514.57 \pm 10.11^{a}$ |
| Evapotranspiration | mm yr$^{-1}$ | $1870.25 \pm 3.21^{a}$ | $1849.44 \pm 2.71^{a}$ | $2152.09 \pm 5.86^{b}$ | $2150.86 \pm 6.97^{b}$ |
| Aridity index | | $0.51 \pm 0.01^{b}$ | $0.68 \pm 0.02^{c}$ | $0.26 \pm 0.01^{a}$ | $0.26 \pm 0.01^{a}$ |
| *CWD* | mm yr$^{-1}$ | $964.75 \pm 2.26^{b}$ | $921.11 \pm 5.65^{a}$ | $1606.82 \pm 8.48^{a}$ | $1637.86 \pm 13.33^{a}$ |
| No. wet months | No. yr$^{-1}$ | $3.50 \pm 0.10^{b}$ | $4 \pm 0.06^{b}$ | $0.18 \pm 0.05^{a}$ | $0.14 \pm 0.05^{a}$ |
| $N_{\text{soil}}$ | mm yr$^{-1}$ | $178.50 \pm 5.87^{a}$ | $179.2 \pm 4.49^{a}$ | $149.42 \pm 3.66^{a}$ | $147.2 \pm 4.72^{a}$ |
| $P_{\text{soil}}$ | mm yr$^{-1}$ | $6.67 \pm 0.53^{a}$ | $2.99 \pm 0.29^{a}$ | $5.69 \pm 0.5^{a}$ | $4.23 \pm 0.32^{a}$ |
| $K_{\text{soil}}$ | mm yr$^{-1}$ | $32.52 \pm 1.45^{a}$ | $40.16 \pm 2^{a}$ | $39.91 \pm 2.74^{a}$ | $33.16 \pm 2.31^{a}$ |
| $OC_{\text{soil}}$ | % mass | $0.63 \pm 0.03^{a}$ | $0.61 \pm 0.03^{a}$ | $0.4 \pm 0.03^{a}$ | $0.44 \pm 0.03^{a}$ |

### *5.2.3. Biometric data and plant material*

The field inventories were conducted on each six representative trees per plot during July and September 2017, yielding 186 trees in total. The subsample of trees for wood anatomical and hydraulic measurements was chosen by stratifying the trees in each plot by their diameter and selecting six individuals with a diameter close to the plot average and approximately equidistant to the plot center. For the estimation of biomass, the height (*H*, 6.3 – 19.2 m) was measured with a Vertex IV hypsometer (Haglöf, Sweden), and the diameter at breast height (*DBH*, 8.11 – 31.5 m) was determined with diametric tape at 1.3 m height for each of the selected trees. Sun-exposed branches were cut from each tree using a long-reaching pruner to obtain leaf and branch samples for morphological, chemical and anatomical analyses. In addition, stem cores were collected from the same trees at breast height using an increment borer with 5.15 mm inner diameter (Haglöf, Sweden).

### *5.2.4. Wood density and biomass production*

Wood density ($WD$, g cm$^{-3}$) was derived through the estimation of dry mass and fresh volume from the stem cores collected at breast height. The fresh volume ($v$, cm$^3$) of the cores was determined by Newton's volume equation (Eq. (1)),

$$v = [(A_o + 4A_m + A_i)/6] \times l \tag{1}$$

where $A_o$, $A_m$ and $A_i$ are the cross-sectional areas obtained by $A = \pi D^2 /4$, using the diameter ($D$, cm) measured at outer end, middle and inner end of the core, and $l$ is the core length (cm), all measured with a digital caliper (Mitutoyo, Japan). Wood density was calculated as the ratio of oven-dry mass (105 °C for 72 h) and fresh volume of each core.

Aboveground biomass ($AGB$, kg) of each tree was estimated using R package BIOMASS (Réjou-Méchain et al., 2017), which is based on improved pan-tropical allometric model based on Eq. (2) from Chave et al. (2014):

$$AGB = 0.0673 \times (WD \times DBH^2 \times H)^{0.975} \tag{2}$$

The $AGB$ increment ($AGBI$, kg yr$^{-1}$) was then computed by dividing the estimated $AGB$ of each tree by stand age (yr).

### *5.2.5. Leaf morphological and chemical traits*

From the harvested upper-canopy samples, a complete and intact 50–75 cm long branch was selected (mean diameter ± SE: 14.84 ± 0.15 mm). For each branch, a mature compound leaf was selected and transferred into a labelled polybag. On the same day, all pinnular leaflets of the compound leaf were detached from the rachis and scanned at 200 dpi resolution using a Canon LiDE 120 flatbed scanner to determine total ($A_l$, cm$^2$) and mean leaf area ($A_{leaf}$, cm$^2$). Later, scanned pinnular leaflets were oven-dried at 70 °C for 48 h in the laboratory of the Indian Institute of Soil and Water conservation, Ballari, India, to compute specific leaf area ($SLA$, cm$^2$ g$^{-1}$) and branch-total leaf area (cm$^2$, $SLA$ × dry mass of all leaves (g), including leaves used to determine $SLA$). Leaf surface area was measured using WinFOLIA software (Régent Instruments, Quebec, Canada). In addition, the leaf-to-sapwood area ratio ($A_l$:$A_s$, m$^2$ cm$^{-2}$) was computed using the xylem area of the branches ($A_{xylem}$, mm$^2$), which was highly correlated to the corresponding cross-sectional area ($A_{cross}$, mm$^2$) measured on the wood anatomical cross sections ($A_{xylem}$ =-5.142 + 0.814 × Across; $r = 0.94$, $p < 0.001$, n = 186).

Ground dry leaf samples were analyzed for foliar signatures of $\delta^{13}C$ and $\delta^{15}N$ at the Centre for Stable Isotopes Research and Analyses (KOSI) in Göttingen, Germany, using a DeltaPlus Isotope mass ratio spectrometer (Finnigan MAT, Bremen, Germany), a Conflo III interface (Thermo Electron Corporation, Bremen, Germany) and a NA1110 elemental analyzer (CE-Instruments, Rodano, Milano, Italy) using standard δ notion: $\delta = (Rsample / Rstandard - 1) \times 1000$ (‰).

### *5.2.6. Branch and stem xylem anatomy and hydraulics*

From the samples used for studying leaf morphological and chemical traits, basipetal branch segments were excised for branch anatomical analysis. Semi-thin transverse sections were cut using a sliding microtome (G.S.l.1, Schenkung Dapples, Zürich, Switzerland). Six sections per branch were stained with Safranin-Alcian Blue and mounted on glass slides. An image of a section was digitally captured at 100 × magnification in the stereomicroscope fitted with a digital camera and an automatic mobile stage (SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany). Captured images were processed using Adobe Photoshop CS6 (Version 13.0 × 64, Adobe Systems Incorporated, USA) and ImageJ v1.47v.

Similar to the branch samples, the wood cores used for wood density measurement were first re-hydrated in a water bath for a day, and then sectioned radially (30–40 µm) by using a sliding microtome for stem wood anatomical analyses. Like branch sections, four sections per core were stained, mounted and dried before capturing an image with the stereomicroscope. To keep a uniform area of measurement, only 20 mm length (from outer bark end to inner pith end) of the captured images was processed per sample.

The particle analysis function of ImageJ was used to estimate single and cumulative vessel lumen area and vessel density (branch and stem *VD*, n mm$^{-2}$). Equivalent vessel diameter (*D*, µm) was calculated for each vessel following White (2006) using Eq. (3), where a and b represent major and minor vessel radii, respectively:

$$D = \left(32 \times \frac{(a \times b)^3}{a^2 + b^2}\right)^{\frac{1}{4}} \quad (3)$$

Relative vessel lumen area ($A_{\text{lumen}}$, %), i.e. the lumen-to-sapwood area ratio, was calculated as the percentage of cumulative vessel lumen area ($A_{\text{lumen}}$, mm$^2$) of the total xylem area ($A_{\text{xylem}}$, mm$^2$). Single branch and stem vessel diameters ($D$, µm) were used to calculate hydraulically-weighted vessel diameter ($D_{\text{h}}$, µm) following Sperry et al. (1994) using Eq. (4):

$$D_h = (\Sigma D^5)/(\Sigma D^4) \quad (4)$$

The theoretical hydraulic conductivity ($K_{\text{h}}$, kg m MPa$^{-1}$ s$^{-1}$) was calculated according to the Hagen–Poiseuille equation (Eq. (5)), where $r$ is the vessel radius in m and $\eta$ and $\rho$ are the viscosity (1.002 10$^{-9}$ MPa s$^{-1}$) and density of water at 20 °C (998.2 kg m$^{-3}$), respectively.

$$K_h = (\pi \times \rho \times \Sigma r^4)/(8 \times \eta) \quad (5)$$

The theoretical sapwood area-specific and leaf area-specific hydraulic conductivity (branch and stem $K_{\text{p}}$ and $K_{\text{l}}$, kg m$^{-1}$ MPa$^{-1}$ s$^{-1}$) were subsequently calculated by dividing $K_{\text{h}}$ by the branch or stem core xylem area ($A_{\text{xylem}}$, m$^2$) and leaf area ($A_{\text{l}}$, m$^2$), respectively. For these calculations, the complete branch cross-section was analyzed (mean ± SE of analyzed branch sapwood area: 95.04 ± 2.59 mm$^2$ and branch leaf area 1,036 ± 46 cm$^2$). The number of counted vessels ranged from 1,227 to 8,846 per branch sample and from 297 to 2,031 per stem sample.

### *5.2.7. Statistical analysis*

All statistical analyses were performed in R (v. 4.0.4; R Core Team, 2021). In order to analyze the joint effect of climate, irrigation treatment, soil properties and biometric traits on a series of tree properties while simultaneously accounting for random plot differences, mixed effects models were fitted using R package lme4 (Bates et al., 2015).

Prior to analysis, all strictly positive variables were natural log transformed to ensure normality of residuals. All numeric variables were subsequently scaled and centered to ease the comparison of regression parameters. To reduce the number of variables in the model (cf. Fig. 5, Fig. 5S1), we decided a priori to limit the analysis of soil variables to nitrogen and phosphorus content (two important indicators of soil nutrient availability), and to use the climatological water deficit (which integrates both precipitation- and temperature-related components of climatic water availability) as the sole predictor of climatic water availability. For all models of wood anatomical and leaf traits, we used *CWD*, irrigation treatment and their interaction, $N_{\text{soil}}$ and $P_{\text{soil}}$ content, and tree height as predictor variables, and allowed the intercept to vary randomly between plots to account for location-specific effects not accounted for by our environmental variables. For the model of aboveground biomass increment, we additionally included the effects of $A_l$:$A_s$ ratio and potential hydraulic conductivity of stem and branch wood. As tree height was an input variable for the calculation of *AGBI* (cf. Eq. (2)) and hence very highly correlated, it was not included in the model for that variable. An inspection of pairwise Pearson correlations between the predictor variables in the models (Fig. 5S1) indicated all of the correlations were safely below the value of $\rho \geq 0.7$ commonly reported as a critical threshold for multicollinearity issues (Dormann et al., 2013).

Models were fitted with restricted maximum likelihood. *P*-values for parameter estimates are based on Wald z-tests with degrees of freedom based on Satterthwaite's correction computed via R package lmerTest version 3.1–0 (Kuznetsova et al., 2017). The variance explained by the fixed effects (marginal $R^2$) and by fixed effects and random plot effects together (conditional $R^2$) were computed using R package MuMIn version 1.43.6 (Bartoń, 2020).

## 5.3. Results

### *5.3.1. Aboveground biomass increment*

The differences in tree size were reflected in the observed patterns in aboveground biomass increment, which ranged from on average 9.04 ± 0.74 kg yr$^{-1}$ (mean ± standard error) at dry sites without irrigation to up to 29.56 ± 0.74 kg yr$^{-1}$ at irrigated, wet sites (Table 5S1, Fig. 5.2). The linear mixed effects model of aboveground biomass increment (Table 5S2) explained about 85% of the variance in *AGBI* for the sites in the analyzed dataset, and around 50% of the variance when predicting to an 'average' site (conditional and marginal $R^2$ of 0.85 and 0.50, respectively). It indicated a significant positive effect of both *CWD* and irrigation on *AGBI*, while their interaction had a negative effect whose magnitude was sufficient to almost completely counteract the irrigation effect in the wet sites (Fig. 5.3, Table 5S2). Accordingly, a more negative *CWD* resulted in reduced wood production, but only if the sites were not irrigated. When comparing trees growing under the same levels of water availability, *AGBI* was higher at higher levels of soil phosphorus availability, and for trees with higher stem $K_p$, while it was not significantly associated with nitrogen availability, branch $K_p$ and the $A_l$:$A_s$ ratio (Fig. 5.3, Table 5S2).

### *5.3.2. Wood anatomy and hydraulic traits*

The response of wood anatomical variables to differences in water availability was not consistent between stems and branches. Stem wood anatomical traits were more responsive to differences in water availability and soil properties than branch wood anatomical traits (Figs. 5.2, 5.4; Table 5S1). Stem vessel diameter (*D*) was higher at wetter sites (though marginally significantly less so if irrigated) and at sites with higher soil *P* contents, and marginally lower for taller trees (Fig. 5.4, Table 5S2). Stem vessel density (*VD*) showed an opposite pattern, with lower values at wetter sites (though significantly less so if irrigated) and at sites with higher phosphorus availability, and marginally higher values for taller trees (Fig. 5.4, Table 5S2). Stem potential conductivity ($K_p$) did not show a strong signal of site conditions, with a marginal $R^2$ of only 0.09 (compared to 0.22 and 0.38 respectively for *D* and *VD*), though there was evidence for a significantly higher stem $K_p$ at irrigated sites (Fig. 5.4, Table 5S2).

For branch wood anatomical traits, besides a significant negative effect of soil *P* on branch *VD*, there were no significant effects on any of the variables, and specifically for sapwood- and leaf-area specific conductivity, the variance explained by the fixed effects was low (marginal $R^2$ of 0.04 and 0.16 for $K_p$ and $K_l$, respectively; Fig. 5.4, Table 5S2). Notably, after accounting for the effect of the other predictor variables, neither tree height nor soil nitrogen content had a significant effect on any of the wood anatomical variables (Fig. 5.4, Table 5S2).

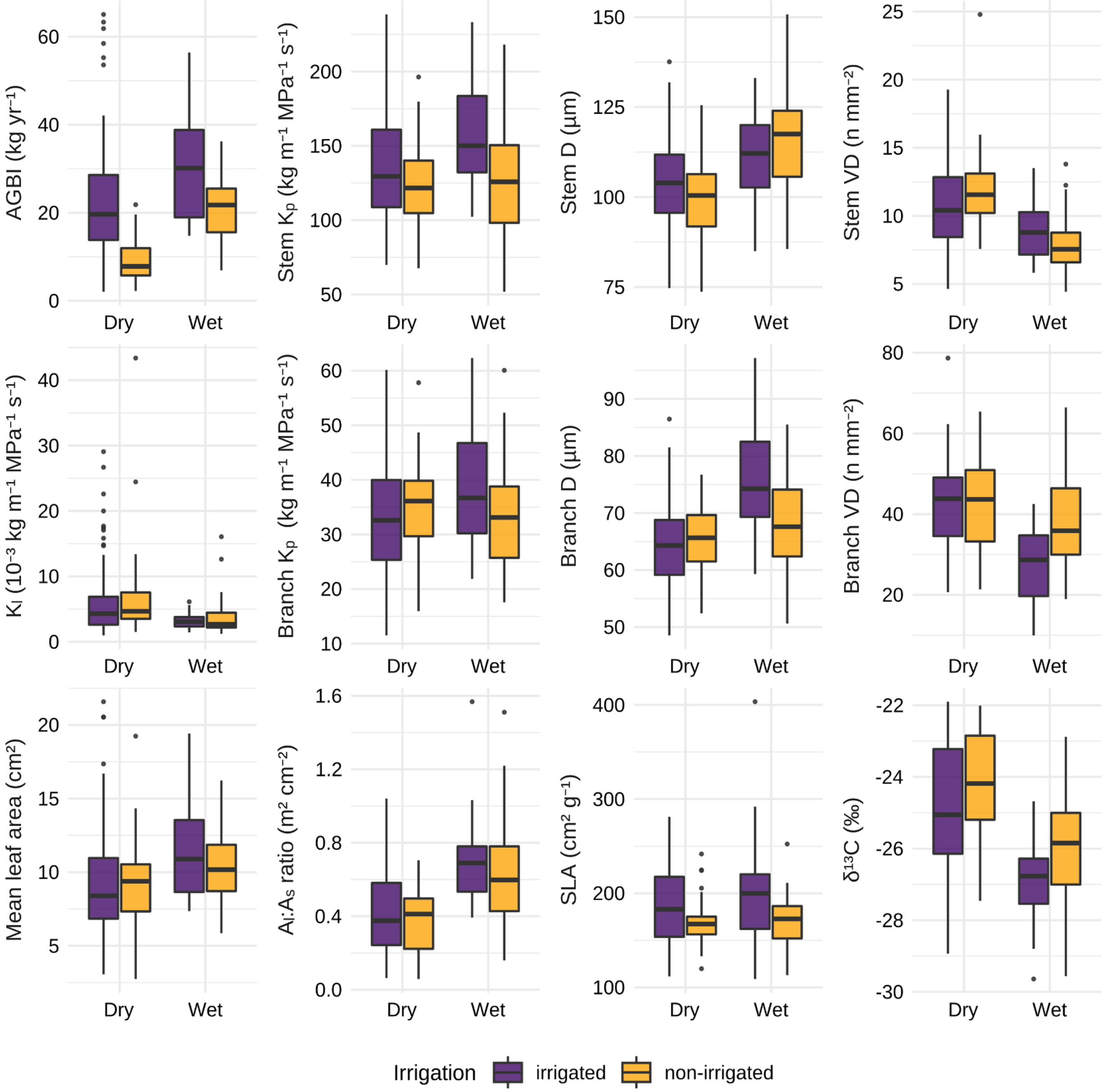

**Fig. 5.2.** Aboveground biomass increment, wood anatomical and leaf traits of trees in the irrigated vs. non-irrigated *Melia dubia* plots. See Table 5.1 for acronyms. For inference on differences between irrigated and non-irrigated plots and different rainfall regimes, see Table 5S2.

### *5.3.3. Leaf traits*

Mean leaf area ($A_{leaf}$) – and hence the $A_l$:$A_s$ ratio – were higher and $\delta^{13}$C lower at wet sites, while specific leaf area (*SLA*) tended to be higher at irrigated sites (Table 5.2, Fig. 5.2). Besides a negative effect of *CWD* on leaf $\delta^{13}$C and a marginally significant positive effect of *CWD* on

$A_{\mathrm{leaf}}$, leaf traits did not have significant associations with water availability related variables (Fig. 5.5, Table 5S2). In general, the fixed effects only explained a relatively low proportion of variance in leaf traits, with marginal $R^2$ values ranging from 0.08 (*SLA*) to 0.34 ($\delta^{13}$C) (Table 5S2). However, the $A_l$:$A_s$ ratio was significantly positively associated with tree height, i.e. taller trees tended to have a higher leaf area per each unit of sapwood area (Fig. 5.5, Table 5S2).

## 5.4. Discussion

### 5.4.1. Influence of water & soil nutrient availability on the growth performance

According to our results, water availability is the most important determinant of biomass accumulation rates of *M. dubia*. Across non-irrigated plantations, average aboveground biomass increment (*AGBI*) rates were about two-fold higher at wet sites than at dry sites (Table 5.2). Adoption of a continuous irrigation scheme further increased *AGBI* more than 2.5-fold at dry sites and 1.4-fold at wet sites (Table 5.2). Trees at irrigated sites in dry regions even achieved higher *AGBI* than at non-irrigated wet sites (Table 5.2, Fig. 5.2), highlighting the potential gains in yield in *M. dubia* plantations that can be achieved by irrigation. However, the highly significant negative interaction between irrigation and climatological water balance (Fig. 5.3, Table 5S2) underlines that the positive effect of irrigation on growth is restricted to sites where plant growth is limited by low precipitation. In agreement with our first hypothesis and findings from previous studies, our results indicate water availability to be the main decisive factor for the growth rate of tropical trees (cf. Toledo et al., 2011; Wagner et al., 2012 and 2014; Guan et al., 2015). Likewise, the positive effect of irrigation on tree growth is in agreement with former studies performed on plantation tree species (c.f. Hunter, 2001; Coyle and Coleman, 2005; Campoe et al., 2013; Pérez-Cruzado et al., 2014). For instance, at irrigated sites, substantially enhanced water use and *AGBI* (up to 26.2 Mg $ha^{-1}$ $yr^{-1}$) were reported for two fast-growing *Eucalyptus* species (Hubbard et al., 2010; Minhas et al., 2015).

Besides water availability, soil nutrient availability limits plant growth (Razaq et al., 2017). Our model accounted for the effects of soil nitrogen and phosphorus content, two macronutrients that are known to limit plant growth (Goldstein et al., 2013; Turner et al., 2018). While we found a positive association between $P_{\mathrm{soil}}$ and *AGBI* ($p < 0.05$; Fig. 5.3; Table 5S2), there was no significant influence of $N_{soil}$. The faster growth at sites with higher phosphorus availability is in line with the longstanding assumption that growth in strongly weathered tropical soils is predominantly phosphorus-limited (Vitousek, 1984; Vitousek and Sanford, 1986). Moreover, differences in soil wetting and redox conditions may alter $P_{soil}$ availability (Ippolito et al., 2019), thus linking the effects of water availability and soil nutrient contents. In either case, the effect size of $P_{soil}$ on *AGBI* was relatively small compared to the effect of water availability (Fig. 5.3, Table 5S2), in agreement with several previous studies showing no to moderate effects of soil characteristics on the growth of tropical trees (Toledo et al., 2011; Alvarez-Clare et al., 2013; Soong et al., 2020). Nevertheless, our results suggest a potential phosphorus limitation of *M. dubia*, and highlight the need to further investigate the nutritional requirements of *M. dubia* to identify suitable site conditions and improve recommendations for fertilizer application.

### *5.4.2. Effects of water availability and tree height on wood anatomical traits*

While we observed the hypothesized effect of water availability on wood anatomical traits at the stem base, no comparable signal was present in the branches (Fig. 5.4, Table 5S2). Specifically, stem vessel diameter was significantly lower at sites with a larger climatological water deficit, and marginally significantly less so when irrigated, while branch vessel diameter was largely unresponsive to water availability. Conduit size has traditionally been explained by climate based on the assumption that trees in dry environments construct narrower conduits than trees in wet environments (Carlquist 1977; Chenlemuge et al., 2015; Pfautsch et al., 2016; Hacke et al., 2017). A large body of literature suggests that narrow conduits are more resistant to embolism under conditions of water limitation (cf. Maherali et al., 2006; Domec et al., 2010; Hajek et al., 2014), which could act as a strong selective force favoring individuals with narrow conduits in dry environments, both within (Liang et al., 2019; Schreiber et al., 2015; Schuldt et al., 2016; Warwick et al., 2017) and across species (Pfautsch et al., 2016; Larter et al., 2017). In this framing, conduit size variation may be viewed as a limited, probably temporal, environmental response exhibited by trees when exposed to dry climates. However, conduit size undergoes considerable changes within individuals along the course of the flow path, which makes its relationship with water availability hard to interpret without taking into account tree height (Olson and Rosell, 2013). In order to compensate for the pressure-drop resulting over the increasing distance from the transpiration sites, vessel diameters have to increase with the length of the flow path (Anfodillo et al. 2006). As tree height is strongly associated with water availability (Moles et al., 2009; Chenlemuge et al., 2015), the observed patterns in stem vessel dimensions may therefore be an indirect consequence of a strongly conserved, relatively static scaling with tree height rather than a direct response to climate, while the xylem traits of terminal branches are relatively strongly conserved (Petit and Anfodillo, 2011; Olson et al., 2021). This may explain the lack of signal in the branch xylem anatomy data (Fig. 5.4, Table 5S2). In this view, water availability limits how high a tree can be, and the height of the tree dictates the size of the vessels at its stem base. For that reason, it has been proposed to standardize vessel diameters based on scaling coefficients from hydraulic optimality models to account for height effects for studies aiming to recognize the relation between vessel diameter and climate (Olson et al., 2021). However, in the present case, there was no positive relationship between height and vessel diameter conditional on water availability; rather, the marginally significant negative effect of tree height on vessel diameter on a log–log-scale implies a scaling relationship with a power of –0.2 (Table 5S2). Standardization for flow path length with a scaling coefficient of 0.2 as proposed by Olson et al. (2021) would therefore have inflated the effect of water availability rather than attenuating it. This illustrates that even though a large part of the variability in conduit dimensions within individuals is likely explained by relatively static scaling laws, a signal of water availability beyond the indirect effect via tree height can still be present in stem wood anatomy data.

The reduced conduit diameter at locations with a more intense climatological water deficit was accompanied by higher vessel densities, though vessel density also was significantly higher at irrigated wet sites (Fig. 5.4, Table 5S1). While a reduction of vessel density towards sites with higher water availability has often been documented (Carlquist 1977; Pfautsch et al. 2016), the pattern at irrigated sites in comparatively wetter biomes is unexpected. A likely explanation is that the continuous water supply at irrigated sites allowed plantation trees to continue their cambial activity and xylogenesis into the dry season, during which they produced relatively smaller and more abundant conduits (Priya and Bhat, 1999; Rossi et al., 2014).

Driven by the effect of water availability on stem vessel diameter and density, stem $K_\mathrm{p}$ was significantly higher at irrigated sites. Branch $K_\mathrm{p}$, on the other hand, was not significantly associated with any of the predictors in the dataset, likely due to the relatively strongly conserved scaling of vessel diameters at terminal branches (Olson et al., 2021).

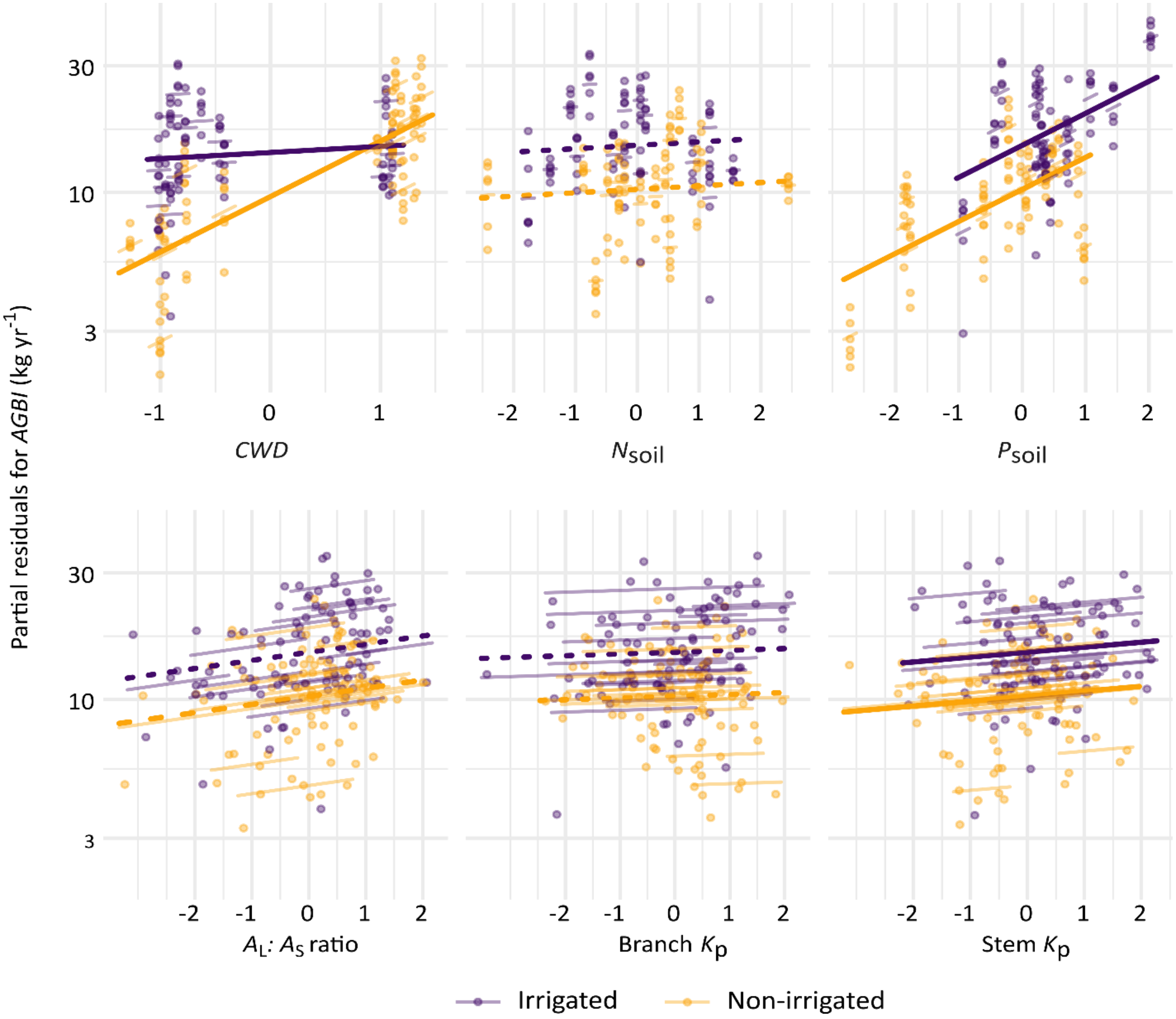

**Fig. 5.3.** Partial residual plots for the model for annual aboveground biomass increment. Shown are counterfactual model predictions when changing the values of one predictor and keeping the others at their average value (lines) overlaid with the partial residuals (points). Colors indicate the irrigation status (purple: irrigated, yellow: non-irrigated); solid lines indicate significant relationships. See Table 5.1 for acronyms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### *5.4.3. Leaf morphological adjustments in response to climatic aridity*

In contrast to our third hypothesis, neither mean leaf area nor specific leaf area was adjusted in response to an increase in climatic aridity. Likewise, observed differences in the leaf-to-sapwood area ratio ($A_l$:$A_s$ ratio) between dry and wet regions (Fig. 5.2) were most likely driven by differences in tree height according to our model and not water availability (Fig. 5.5). In tropical trees, the $A_l$:$A_s$ ratio commonly declines with height in the canopy (Schuldt et al., 2011). We originally assumed that the $A_l$:$A_s$ ratio as a key variable of a plant's water balance would respond plastically to changes in water availability, in conjunction with other intra-specific studies along environmental gradients (Martinez-Vilalta et al., 2009; Rosas et al., 2019; Lopez et al., 2021). We speculate that *M. dubia* as a drought-deciduous species is simply shedding its leaves triggered by a certain level of drought exposure instead of modifying its structural properties to adapt to changing levels of water availability (cf. Choat et al., 2005; Hoeber et al., 2014). Such a drought-avoiding isohydric strategy (cf. Brodribb et al., 2003) would explain the observed weak relationship between leaf traits and water availability in our study (Fig. 5.5). Notwithstanding, in agreement with hypothesis (iv), the observed patterns in leaf stable isotope signatures ($\delta^{13}C$) suggest a stronger water limitation of photosynthesis at sites with a more negative water balance, and are consistent with a higher water use efficiency at these sites.

### *5.4.4. Influence of wood properties and leaf traits on growth performance*

We found a significant relationship between *AGBI* and stem $K_p$ ($p < 0.05$), but not with branch $K_p$ (Fig. 5.3; Table 5S2). Our results confirm the assumption by Tyree (2003) who hypothesized that 'high plant hydraulic conductance is necessary for high productivity in forest trees'. They are further consistent with reports that tree growth rate is strongly linked to stem $K_p$ and thus to tree size across species (Zhang and Cao, 2009; Poorter et al., 2010; Russo et al., 2010; Fan et al., 2012; Kotowska et al., 2021), but not necessarily to branch $K_p$, although mixed results exist (cf. Hajek et al., 2014; Hoeber et al., 2014; Kotowska et al., 2015).

On irrigated sites, a higher stem $K_p$ also had a significant positive effect on *AGBI* (Fig. 5.3, Table 5S2), confirming the suggested influence of wood hydraulic properties on growth (cf. Tyree, 2003; Brodribb, 2009). However, the weak relationship between stem $K_p$ with climate indicates that this link is not sufficient to explain the observed patterns in *AGBI*, which likely are also strongly affected by the prolonged or even continuous cambial activity and xylogenesis on wetter sites (Priya and Bhat, 1999; Rossi et al., 2014).

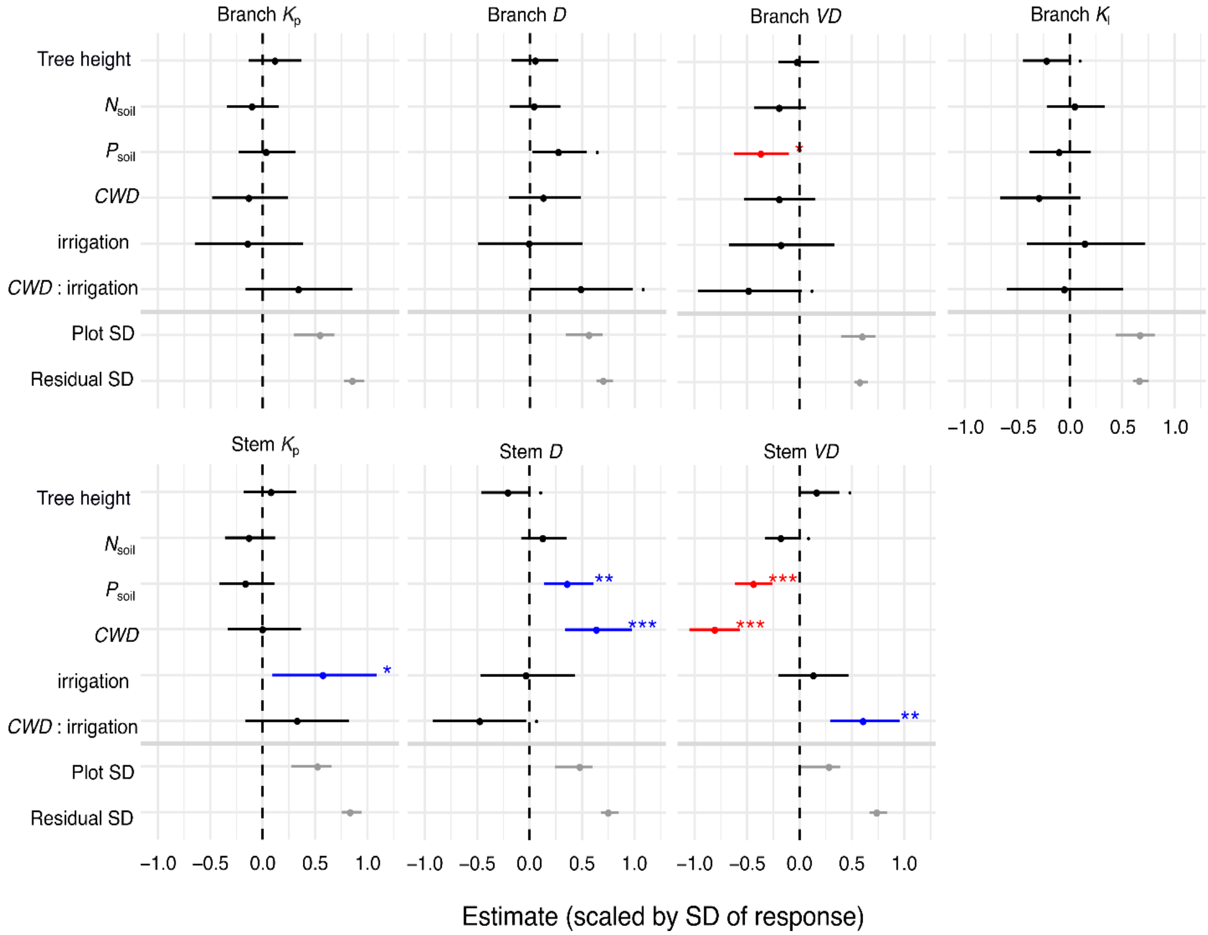

**Fig. 5.4**. Estimated effect sizes in the models of branch and stem wood anatomic and hydraulic traits (see Table 5.1 for acronyms). Shown are the estimates (scaled as changes in standard deviations of the response when changing the predictor by one standard deviation) with their 95% confidence intervals. Colors of the fixed effects estimates indicate significant ($p \leq 0.05$) negative (red) and positive (blue) effects and insignificant effects (black). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.

The higher *AGBI* on soils with a high *P* content was accompanied by an increase in stem vessel diameter and reductions in branch and stem vessel density. This is consistent with the described increase in vessel diameter with nutrient availability, mainly nitrogen (Hacke et al. 2010; Plavcová et al. 2013; Spannl et al., 2016) and may reflect a shift to a more efficient xylem anatomy precipitated by the more favorable nutrient availability (Goldstein et al., 2013; Hacke et al., 2017). Most likely, nutrients alter wood anatomical and hydraulic traits due to their link to growth rates (Ewers et al., 2001; Phillips et al., 2001; Giardina et al., 2003; Amponsah et al. 2004; Lovelock et al., 2004; Bucci et al., 2006; B´aez and Homeier, 2018). In *M. dubia*, greater $P_{soil}$ control of stem vessel diameter (Fig. 5.4, Table 5S2) appears to be a species-specific strategy towards soil nutrient regimes (Faustino et al., 2013; Goldstein et al., 2013).

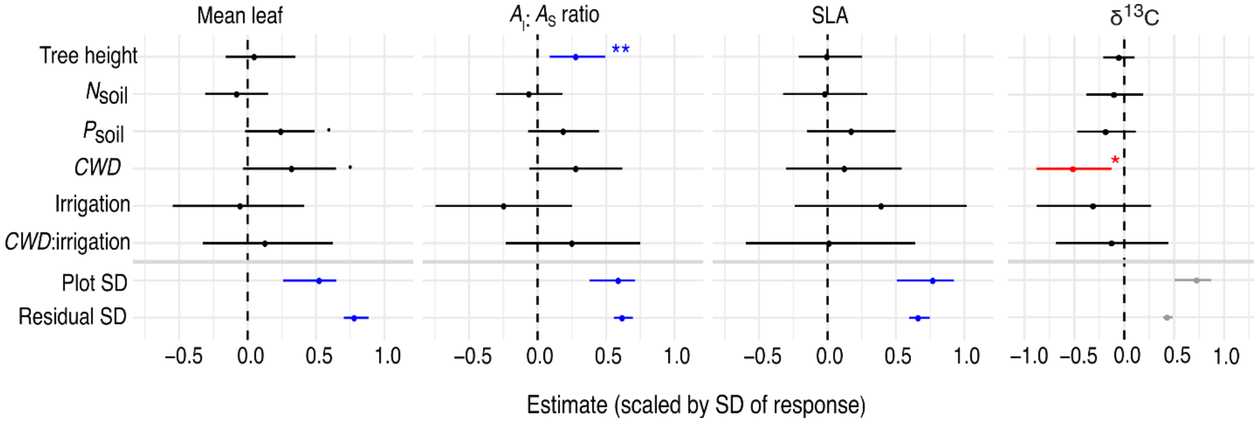

**Fig. 5.5.** Estimated effect sizes in the models of leaf morphological traits and $\delta^{13}C$ signals (see Table 1 for acronyms). Shown are the estimates (scaled as changes in standard deviations of the response when changing the predictor by one standard deviation) with their 95% confidence intervals. Colors of the fixed-effects estimates indicate significant ($p \leq 0.05$) negative (red) and positive (blue) effects and insignificant effects (black). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We assumed to find a close relationship between given leaf-area related traits and the growth patterns across our gradient. Although these leaf traits are known to be associated with the resource acquisition strategy, we did not observe any relationship. In agreement hereon, several studies likewise could not confirm any connection between leaf traits and growth performance (Poorter, et al., 2008; Wright et al., 2010; Hérault et al., 2011; Paine et al., 2015;

Guimarães et al., 2018). Further, it was found that leaf traits were not correlated consistently with growth rates throughout the lifetime of trees (Gibert et al., 2016; Falster et al., 2018). Thus, the observed pairwise correlation between the $A_l$:$A_s$ ratio and *AGBI* (Fig. 5S1) was most likely driven by confounding tree height effects, which explains why our model did not confirm any significant effects of $A_l$:$A_s$ on *AGBI*.

## 5.5. Conclusions

Our analysis indicates water availability to be a major driver of the biomass productivity of *M. dubia*, with a strong positive association between *AGBI* and water availability. Irrigation, however, was most effective at sites on the dryer end of the covered precipitation gradient. The increased biomass productivity at sites with higher water availability was accompanied by increases in stem vessel diameter and hydraulic conductivity, while branch wood anatomy was largely unrelated to water availability and soil conditions. Notably, as these patterns in stem wood anatomy persisted when accounting for flow path length, they are unlikely to arise indirectly from differences in stem length alone. Leaf traits were largely unrelated to water availability, likely owing to the drought-deciduous nature of the species. Our results on the effects of soil phosphorus availability further suggest a role of soil chemistry for the growth and stem wood anatomy of *M. dubia* that is consistent with a phosphorus limitation in at least a subset of sites. We therefore conclude that to improve the yield of *M. dubia* in short-rotation plantations, further research should focus on the benefits of irrigation (specifically in regions which receive annual precipitation considerably lower than 1,000 mm $yr^{-1}$) and of phosphorus supplementation on poor soils.

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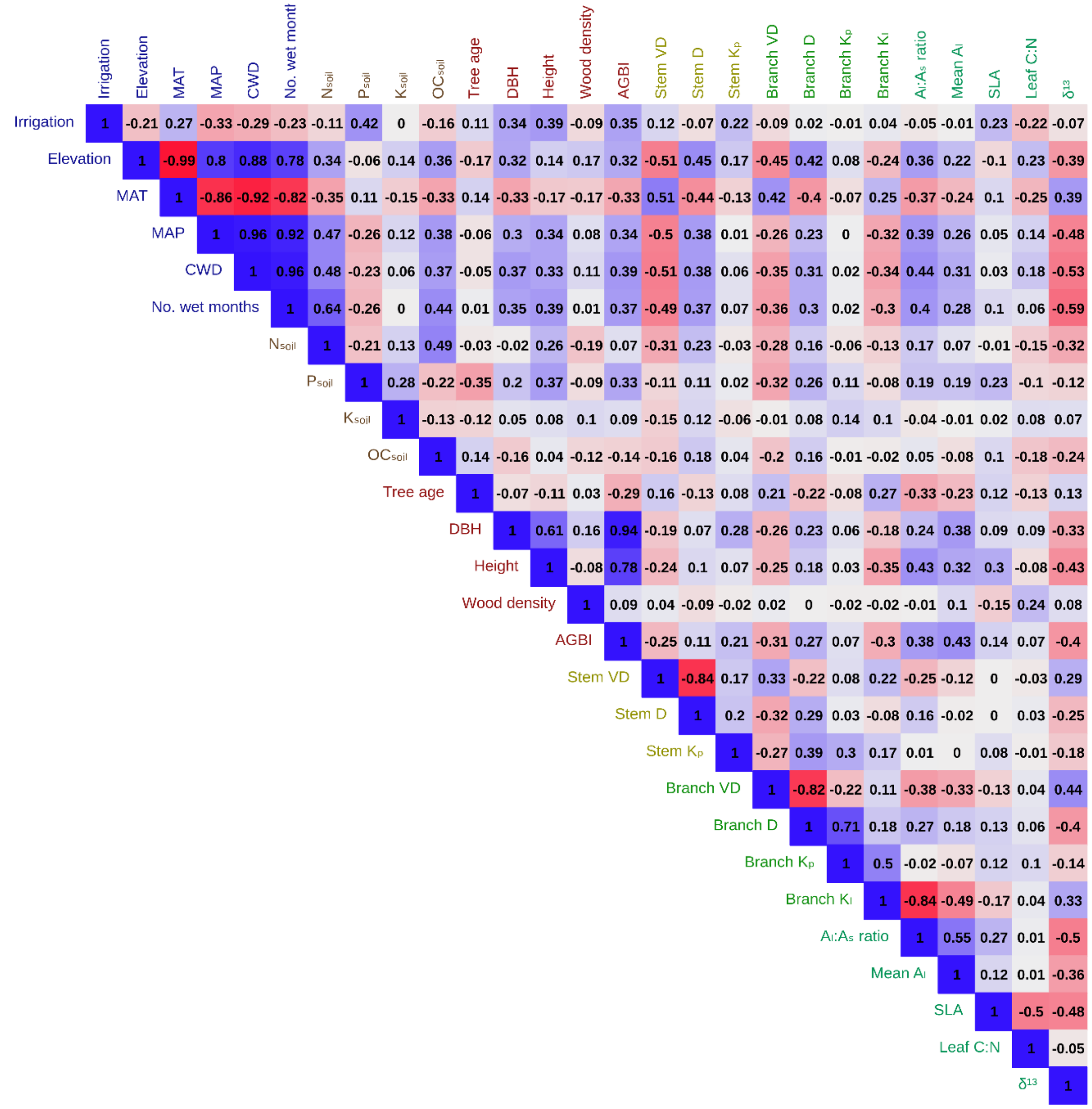
## 5.7. Appendix: Supplementary material of Chapter 5



| | Irrigation | Elevation | MAT | MAP | CWD | No. wet mont | $N_{soil}$ | $P_{soil}$ | $K_{soil}$ | $OC_{soil}$ | Tree age | DBH | Height | Wood density | AGBI | Stem VD | Stem D | Stem $K_p$ | Branch VD | Branch D | Branch $K_p$ | Branch $K_l$ | $A_l$:$A_s$ ratio | Mean $A_l$ | SLA | Leaf C:N | $\delta^{13}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Irrigation | 1 | -0.21 | 0.27 | -0.33 | -0.29 | -0.23 | -0.11 | 0.42 | 0 | -0.16 | 0.11 | 0.34 | 0.39 | -0.09 | 0.35 | 0.12 | -0.07 | 0.22 | -0.09 | 0.02 | -0.01 | 0.04 | -0.05 | -0.01 | 0.23 | -0.22 | -0.07 |
| Elevation | | 1 | -0.99 | 0.8 | 0.88 | 0.78 | 0.34 | -0.06 | 0.14 | 0.36 | -0.17 | 0.32 | 0.14 | 0.17 | 0.32 | -0.51 | 0.45 | 0.17 | -0.45 | 0.42 | 0.08 | -0.24 | 0.36 | 0.22 | -0.1 | 0.23 | -0.39 |
| MAT | | | 1 | -0.86 | -0.92 | -0.82 | -0.35 | 0.11 | -0.15 | -0.33 | 0.14 | -0.33 | -0.17 | -0.17 | -0.33 | 0.51 | -0.44 | -0.13 | 0.42 | -0.4 | -0.07 | 0.25 | -0.37 | -0.24 | 0.1 | -0.25 | 0.39 |
| MAP | | | | 1 | 0.96 | 0.92 | 0.47 | -0.26 | 0.12 | 0.38 | -0.06 | 0.3 | 0.34 | 0.08 | 0.34 | -0.5 | 0.38 | 0.01 | -0.26 | 0.23 | 0 | -0.32 | 0.39 | 0.26 | 0.05 | 0.14 | -0.48 |
| CWD | | | | | 1 | 0.96 | 0.48 | -0.23 | 0.06 | 0.37 | -0.05 | 0.37 | 0.33 | 0.11 | 0.39 | -0.51 | 0.38 | 0.06 | -0.35 | 0.31 | 0.02 | -0.34 | 0.44 | 0.31 | 0.03 | 0.18 | -0.53 |
| No. wet months | | | | | | 1 | 0.64 | -0.26 | 0 | 0.44 | 0.01 | 0.35 | 0.39 | 0.01 | 0.37 | -0.49 | 0.37 | 0.07 | -0.36 | 0.3 | 0.02 | -0.3 | 0.4 | 0.28 | 0.1 | 0.06 | -0.59 |
| $N_{soil}$ | | | | | | | 1 | -0.21 | 0.13 | 0.49 | -0.03 | -0.02 | 0.26 | -0.19 | 0.07 | -0.31 | 0.23 | -0.03 | -0.28 | 0.16 | -0.06 | -0.13 | 0.17 | 0.07 | -0.01 | -0.15 | -0.32 |
| $P_{soil}$ | | | | | | | | 1 | 0.28 | -0.22 | -0.35 | 0.2 | 0.37 | -0.09 | 0.33 | -0.11 | 0.11 | 0.02 | -0.32 | 0.26 | 0.11 | -0.08 | 0.19 | 0.19 | 0.23 | -0.1 | -0.12 |
| $K_{soil}$ | | | | | | | | | 1 | -0.13 | -0.12 | 0.05 | 0.08 | 0.1 | 0.09 | -0.15 | 0.12 | -0.06 | -0.01 | 0.08 | 0.14 | 0.1 | -0.04 | -0.01 | 0.02 | 0.08 | 0.07 |
| $OC_{soil}$ | | | | | | | | | | 1 | 0.14 | -0.16 | 0.04 | -0.12 | -0.14 | -0.16 | 0.18 | 0.04 | -0.2 | 0.16 | -0.01 | -0.02 | 0.05 | -0.08 | 0.1 | -0.18 | -0.24 |
| Tree age | | | | | | | | | | | 1 | -0.07 | -0.11 | 0.03 | -0.29 | 0.16 | -0.13 | 0.08 | 0.21 | -0.22 | -0.08 | 0.27 | -0.33 | -0.23 | 0.12 | -0.13 | 0.13 |
| DBH | | | | | | | | | | | | 1 | 0.61 | 0.16 | 0.94 | -0.19 | 0.07 | 0.28 | -0.26 | 0.23 | 0.06 | -0.18 | 0.24 | 0.38 | 0.09 | 0.09 | -0.33 |
| Height | | | | | | | | | | | | | 1 | -0.08 | 0.78 | -0.24 | 0.1 | 0.07 | -0.25 | 0.18 | 0.03 | -0.35 | 0.43 | 0.32 | 0.3 | -0.08 | -0.43 |
| Wood density | | | | | | | | | | | | | | 1 | 0.09 | 0.04 | -0.09 | -0.02 | 0.02 | 0 | -0.02 | -0.02 | -0.01 | 0.1 | -0.15 | 0.24 | 0.08 |
| AGBI | | | | | | | | | | | | | | | 1 | -0.25 | 0.11 | 0.21 | -0.31 | 0.27 | 0.07 | -0.3 | 0.38 | 0.43 | 0.14 | 0.07 | -0.4 |
| Stem VD | | | | | | | | | | | | | | | | 1 | -0.84 | 0.17 | 0.33 | -0.22 | 0.08 | 0.22 | -0.25 | -0.12 | 0 | -0.03 | 0.29 |
| Stem D | | | | | | | | | | | | | | | | | 1 | 0.2 | -0.32 | 0.29 | 0.03 | -0.08 | 0.16 | -0.02 | 0 | 0.03 | -0.25 |
| Stem $K_p$ | | | | | | | | | | | | | | | | | | 1 | -0.27 | 0.39 | 0.3 | 0.17 | 0.01 | 0 | 0.08 | -0.01 | -0.18 |
| Branch VD | | | | | | | | | | | | | | | | | | | 1 | -0.82 | -0.22 | 0.11 | -0.38 | -0.33 | -0.13 | 0.04 | 0.44 |
| Branch D | | | | | | | | | | | | | | | | | | | | 1 | 0.71 | 0.18 | 0.27 | 0.18 | 0.13 | 0.06 | -0.4 |
| Branch $K_p$ | | | | | | | | | | | | | | | | | | | | | 1 | 0.5 | -0.02 | -0.07 | 0.12 | 0.1 | -0.14 |
| Branch $K_l$ | | | | | | | | | | | | | | | | | | | | | | 1 | -0.84 | -0.49 | -0.17 | 0.04 | 0.33 |
| $A_l$:$A_s$ ratio | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.55 | 0.27 | 0.01 | -0.5 |
| Mean $A_l$ | | | | | | | | | | | | | | | | | | | | | | | | 1 | 0.12 | 0.01 | -0.36 |
| SLA | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.5 | -0.48 |
| Leaf C:N | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | -0.05 |
| $\delta^{13}$ | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |

**Fig. 5S1.** Pearson's correlation coefficients for climatic and soil predictors and stem, branch and leaf anatomical and hydraulic traits. Blue: positive correlation, red: negative correlation.

**Table 5S1.** Summary of all major variables explored. Given are the means ± SE for wet and dry regions, separated between irrigated and non-irrigated sites.

| Variable | Unit | Wet (>1000 mm *MAP*) | | Dry (< 700 mm *MAP*) | |
|---|---|---|---|---|---|
| | | Irrigated | Non-irrigated | Irrigated | Non-irrigated |
| *AGBI* | ($kg\ yr^{-1}$) | 29.56 ± 2.46 | 20.97 ± 1.01 | 23.13 ± 1.8 | 9.04 ± 0.74 |
| stem vessel diameter | (µm) | 111.52 ± 2.75 | 114.72 ± 1.97 | 104.13 ± 1.63 | 99.8 ± 1.48 |
| Stem vessel density | ($n\ mm^{-2}$) | 8.98 ± 0.44 | 7.97 ± 0.28 | 10.73 ± 0.37 | 11.83 ± 0.45 |
| Stem $D_h$ | µm | 213.88 ± 2.85 | 200.89 ± 1.92 | 197.63 ± 1.84 | 187.65 ± 2.77 |
| Stem $K_p$ | ($kg\ m^{-1}\ MPa^{-1}\ s^{-1}$) | 158.13 ± 7.92 | 126.36 ± 5.14 | 135.44 ± 4.71 | 122.41 ± 4.59 |
| Branch vessel diameter | (µm) | 77.18 ± 2.27 | 68.04 ± 1.19 | 64.11 ± 0.98 | 65.46 ± 0.94 |
| Branch vessel density | ($n\ mm^{-2}$) | 27.28 ± 2.05 | 38.44 ± 1.59 | 42.95 ± 1.34 | 42.52 ± 1.57 |
| Branch $D_h$ | µm | 102.48 ± 2.54 | 90.57 ± 1.38 | 89.69 ± 1.16 | 91 ± 1.28 |
| Branch $K_p$ | ($kg\ m^{-1}\ MPa^{-1}\ s^{-1}$) | 37.89 ± 2.13 | 33.77 ± 1.35 | 33.36 ± 1.31 | 34.97 ± 1.3 |
| Branch $K_l$ | ($10^{-4} kg\ m^{-1}\ MPa^{-1}\ s^{-1}$) | 3.28 ± 0.24 | 3.63 ± 0.37 | 6.51 ± 0.78 | 6.98 ± 1.11 |
| $A_{leaf}$ | ($cm^2$) | 11.61 ± 0.69 | 10.36 ± 0.34 | 9.43 ± 0.49 | 9.08 ± 0.47 |
| $A_l$: $A_s$ | ( $m^2\ cm^{-2}$) | 0.70 ± 0.05 | 0.62 ± 0.04 | 0.44 ± 0.03 | 0.38 ± 0.03 |
| *SLA* | ($cm^2\ g^{-1}$) | 199.59 ± 12.78 | 170.18 ± 3.45 | 187.14 ± 5.22 | 169.4 ± 3.73 |
| Leaf C:N | | 11.18 ± 0.32 | 13.01 ± 0.28 | 11.44 ± 0.38 | 11.7 ± 0.43 |
| δ13c | ‰ | -26.92 ± 0.23 | -26.02 ± 0.19 | -24.96 ± 0.21 | -24.24 ± 0.23 |

**Table 5S2.** Parameter estimates of the mixed-effects models with their standard errors, t-values, estimated degrees of freedom (*edf*) based on Satterthwaites approximation and *p*-values. Further reported are the standard deviation of the plot-level random intercepts (Plot *SD*), the residual standard deviation (*RSD*), and the marginal and conditional $R^2$ ($R^2$marg and $R^2$cond, respectively). In the presented models, all numeric predictors besides *CWD* are strictly positive and enter in the natural log scale.

| Response | Term | Estimate | Std. Err. | *t*-value | *edf* | *p*-value | Plot *SD* | *RSD* | $R^2_{marg.}$ | $R^2_{cond.}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| *AGBI* | (Intercept) | -0.391 | 0.169 | -2.319 | 25.2 | 0.029 * | 0.608 | 0.402 | 0.50 | 0.85 |
| | *CWD* | 0.778 | 0.168 | 4.638 | 26.0 | < 0.001 *** | | | | |
| | Irrigation | 0.644 | 0.262 | 2.458 | 25.4 | 0.021 * | | | | |
| | $N_{soil}$ | -0.099 | 0.130 | -0.758 | 25.0 | 0.455 | | | | |
| | $P_{soil}$ | 0.338 | 0.133 | 2.544 | 25.8 | 0.017 * | | | | |
| | $K_p$ (Branch) | 0.014 | 0.038 | 0.384 | 161.2 | 0.702 | | | | |
| | $K_p$ (Stem) | 0.099 | 0.039 | 2.537 | 162.1 | 0.012 * | | | | |
| | $A_l$:$A_s$ | 0.094 | 0.050 | 1.875 | 171.7 | 0.062 . | | | | |
| | *CWD* :Irrigation | -0.549 | 0.255 | -2.155 | 25.1 | 0.041 * | | | | |

**Table 5S2.** (continued).

| Response | Term | Estimate | Std. Err. | *t*-value | *edf* | *p*-value | Plot *SD* | *RSD* | $R^2_{\text{marg.}}$ | $R^2_{\text{cond.}}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Stem vessel diameter | (Intercept) | -0.055 | 0.162 | -0.341 | 25.4 | 0.736 | 0.486 | 0.757 | 0.22 | 0.45 |
| | *CWD* | 0.644 | 0.174 | 3.707 | 31.2 | < 0.001 *** | | | | |
| | Irrigation | -0.027 | 0.250 | -0.108 | 25.5 | 0.915 | | | | |
| | $N_{\text{soil}}$ | 0.133 | 0.121 | 1.101 | 23.3 | 0.282 | | | | |
| | $P_{\text{soil}}$ | 0.366 | 0.131 | 2.790 | 27.7 | 0.009 ** | | | | |
| | Tree height | -0.199 | 0.117 | -1.699 | 119.7 | 0.092 . | | | | |
| | *CWD* :Irrigation | -0.468 | 0.247 | -1.895 | 26.2 | 0.069 . | | | | |
| Stem vessel density | (Intercept) | 0.022 | 0.120 | 0.183 | 26.3 | 0.856 | 0.289 | 0.744 | 0.38 | 0.46 |
| | *CWD* | -0.801 | 0.132 | -6.049 | 31.8 | < 0.001 *** | | | | |
| | Irrigation | 0.139 | 0.186 | 0.751 | 26.3 | 0.459 | | | | |
| | $N_{\text{soil}}$ | -0.170 | 0.089 | -1.923 | 24.1 | 0.066 . | | | | |
| | $P_{\text{soil}}$ | -0.431 | 0.098 | -4.389 | 28.5 | < 0.001 *** | | | | |
| | Tree height | 0.171 | 0.101 | 1.697 | 78.2 | 0.094 . | | | | |
| | *CWD* :Irrigation | 0.614 | 0.184 | 3.337 | 27.0 | 0.002 ** | | | | |
| Stem $K_p$ | (Intercept) | -0.233 | 0.178 | -1.310 | 26.9 | 0.201 | 0.532 | 0.842 | 0.09 | 0.35 |
| | *CWD* | 0.007 | 0.192 | 0.039 | 32.9 | 0.969 | | | | |
| | Irrigation | 0.583 | 0.275 | 2.117 | 26.9 | 0.044 * | | | | |
| | $N_{\text{soil}}$ | -0.122 | 0.133 | -0.918 | 24.7 | 0.367 | | | | |
| | $P_{\text{soil}}$ | -0.155 | 0.144 | -1.076 | 29.2 | 0.291 | | | | |
| | Tree height | 0.088 | 0.130 | 0.676 | 120.4 | 0.500 | | | | |
| | *CWD* :Irrigation | 0.338 | 0.272 | 1.241 | 27.7 | 0.225 | | | | |
| Branch vessel diameter | (Intercept) | 0.072 | 0.178 | 0.405 | 27.3 | 0.689 | 0.571 | 0.708 | 0.24 | 0.54 |
| | *CWD* | 0.137 | 0.188 | 0.729 | 33.0 | 0.471 | | | | |
| | Irrigation | 0.000 | 0.275 | 0.000 | 27.3 | 1.000 | | | | |
| | $N_{\text{soil}}$ | 0.048 | 0.134 | 0.360 | 25.2 | 0.722 | | | | |
| | $P_{\text{soil}}$ | 0.280 | 0.143 | 1.957 | 29.4 | 0.060 . | | | | |
| | Tree height | 0.060 | 0.116 | 0.520 | 149.1 | 0.604 | | | | |
| | *CWD* :Irrigation | 0.495 | 0.271 | 1.822 | 28.0 | 0.079 . | | | | |
| Branch vessel density | (Intercept) | 0.012 | 0.180 | 0.066 | 27.1 | 0.948 | 0.608 | 0.584 | 0.35 | 0.69 |
| | *CWD* | -0.184 | 0.187 | -0.986 | 31.9 | 0.332 | | | | |
| | Irrigation | -0.168 | 0.278 | -0.604 | 27.1 | 0.551 | | | | |
| | $N_{\text{soil}}$ | -0.185 | 0.136 | -1.357 | 25.4 | 0.187 | | | | |
| | $P_{\text{soil}}$ | -0.360 | 0.144 | -2.505 | 28.9 | 0.018 * | | | | |
| | Tree height | -0.015 | 0.101 | -0.144 | 171.2 | 0.886 | | | | |
| | *CWD* :Irrigation | -0.476 | 0.273 | -1.743 | 27.7 | 0.092 . | | | | |
| Branch $K_p$ | (Intercept) | 0.117 | 0.184 | 0.634 | 27.9 | 0.531 | 0.554 | 0.863 | 0.04 | 0.32 |
| | *CWD* | -0.126 | 0.198 | -0.635 | 34.1 | 0.530 | | | | |
| | Irrigation | -0.136 | 0.285 | -0.478 | 27.9 | 0.636 | | | | |
| | $N_{\text{soil}}$ | -0.095 | 0.138 | -0.691 | 25.6 | 0.496 | | | | |
| | $P_{\text{soil}}$ | 0.040 | 0.149 | 0.267 | 30.3 | 0.791 | | | | |
| | Tree height | 0.124 | 0.134 | 0.927 | 123.9 | 0.356 | | | | |
| | *CWD* :Irrigation | 0.349 | 0.282 | 1.239 | 28.7 | 0.225 | | | | |

**Table 5S2.** (continued).

| Response | Term | Estimate | Std. Err. | *t* -value | *edf* | *p* -value | Plot *SD* | *RSD* | $R^2_{marg.}$ | $R^2_{cond.}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Branch $K_l$ | (Intercept) | -0.080 | 0.202 | -0.397 | 27.0 | 0.695 | 0.679 | 0.672 | 0.16 | 0.58 |
| | *CWD* | -0.284 | 0.210 | -1.354 | 32.0 | 0.185 | | | | |
| | Irrigation | 0.152 | 0.312 | 0.488 | 27.0 | 0.629 | | | | |
| | $N_{soil}$ | 0.056 | 0.153 | 0.369 | 25.3 | 0.715 | | | | |
| | $P_{soil}$ | -0.094 | 0.161 | -0.580 | 28.9 | 0.567 | | | | |
| | Tree height | -0.212 | 0.116 | -1.836 | 169.2 | 0.068 . | | | | |
| | *CWD* :Irrigation | -0.043 | 0.307 | -0.141 | 27.6 | 0.889 | | | | |
| Mean leaf area | (Intercept) | 0.044 | 0.172 | 0.254 | 23.7 | 0.801 | 0.526 | 0.782 | 0.17 | 0.43 |
| | *CWD* | 0.325 | 0.185 | 1.758 | 29.1 | 0.089 . | | | | |
| | Irrigation | -0.051 | 0.267 | -0.192 | 23.7 | 0.849 | | | | |
| | $N_{soil}$ | -0.076 | 0.129 | -0.590 | 21.7 | 0.561 | | | | |
| | $P_{soil}$ | 0.246 | 0.140 | 1.764 | 25.8 | 0.090 . | | | | |
| | Tree height | 0.052 | 0.123 | 0.424 | 122.0 | 0.672 | | | | |
| | *CWD* :Irrigation | 0.131 | 0.264 | 0.496 | 24.4 | 0.624 | | | | |
| $A_l$:$A_s$ ratio | (Intercept) | 0.155 | 0.178 | 0.871 | 27.1 | 0.391 | 0.593 | 0.621 | 0.30 | 0.64 |
| | *CWD* | 0.283 | 0.186 | 1.520 | 32.3 | 0.138 | | | | |
| | Irrigation | -0.244 | 0.276 | -0.885 | 27.2 | 0.384 | | | | |
| | $N_{soil}$ | -0.060 | 0.135 | -0.443 | 25.3 | 0.661 | | | | |
| | $P_{soil}$ | 0.191 | 0.143 | 1.341 | 29.1 | 0.190 | | | | |
| | Tree height | 0.283 | 0.106 | 2.678 | 165.2 | 0.008 ** | | | | |
| | *CWD* :Irrigation | 0.255 | 0.271 | 0.940 | 27.8 | 0.355 | | | | |
| *SLA* | (Intercept) | -0.189 | 0.224 | -0.843 | 25.9 | 0.407 | 0.773 | 0.665 | 0.08 | 0.61 |
| | *CWD* | 0.127 | 0.232 | 0.547 | 30.1 | 0.588 | | | | |
| | Irrigation | 0.395 | 0.347 | 1.139 | 25.9 | 0.265 | | | | |
| | $N_{soil}$ | -0.016 | 0.171 | -0.092 | 24.4 | 0.928 | | | | |
| | $P_{soil}$ | 0.177 | 0.179 | 0.989 | 27.5 | 0.331 | | | | |
| | Tree height | -0.001 | 0.117 | -0.005 | 176.2 | 0.996 | | | | |
| | *CWD* :Irrigation | 0.015 | 0.341 | 0.044 | 26.4 | 0.965 | | | | |
| $\delta^{13}C$ | (Intercept) | 0.131 | 0.204 | 0.639 | 26.1 | 0.529 | 0.733 | 0.436 | 0.34 | 0.83 |
| | *CWD* | -0.507 | 0.207 | -2.448 | 28.7 | 0.021 * | | | | |
| | Irrigation | -0.306 | 0.316 | -0.967 | 26.1 | 0.342 | | | | |
| | $N_{soil}$ | -0.096 | 0.157 | -0.610 | 25.2 | 0.548 | | | | |
| | $P_{soil}$ | -0.180 | 0.162 | -1.110 | 27.1 | 0.277 | | | | |
| | Tree height | -0.047 | 0.080 | -0.589 | 176.9 | 0.557 | | | | |
| | *CWD* :Irrigation | -0.120 | 0.310 | -0.387 | 26.4 | 0.702 | | | | |

# Chapter 6: Synthesis

## 6.1. Introduction

Increasing landscape tree cover and carbon sequestration is considered a cost-effective climate change mitigation tool. While a natural secondary succession of native forest tree species is likely the preferred option from an ecological point of view, agroforests, farm woodlots and tree plantations are land-use options that can balance ecological and socio-economic needs. Tree plantations in India and elsewhere in the tropics are often established from a very limited number of ‘classic’, highly productive plantation species. However, recent advances in plantation research advocate to mix fast and slow-growing natives and exotics to derive numerous environmental benefits. However, the knowledge on the performance of potential native species in the tropics is yet to be explored for their deployment in plantations.

## 6.2. Tree biomass estimation

Agroforestry systems (*AFS*) are being considered important carbon stocks (Zomer et al., 2016; Löf et al., 2019) and tree components of the system are being subject of study for exploring the carbon sequestration potential. *M. dubia,* being a one promising tree species in *AFS*, needs an accurate estimation of its biomass production potential. Presently, species-specific biomass-estimation allometrics for *M. dubia* are not available and productivity quantification is also limited to the trees grown in experimental plots (Kirankumar and Patil, 2017; Thakur et al., 2018). The reported farm factor-based biomass estimation methods were crude and require computation of region-specific farm factors. Therefore, identification of reliable allometric model for quick aboveground biomass (*AGB*) estimates is need of the hour for realizing benefits from carbon sequestration, or $CO_2$ emission reduction through the management of terrestrial woody biomass (Chave et al., 2014). Further, the carbon content of the *M. dubia* wood was not analyzed. Hence, in this attempt relatively best-suited biomass estimation models were compared and Chave et al. (2014) *AGB* model was adopted. The *AFS* are being assessed and counted in the global and national carbon budget (Zomer et al., 2016; Betemariyam et al., 2020) and thus an accurate estimate of *AGB* is required for the implementation of REDD+ initiatives with better understanding of the carbon cycle components in the *AFS* (Campioli et al., 2016; Betemariyam et al., 2020).

## 6.3. Planting geometry and tree growth

The farmers growing *M. dubia* in Southern India have adopted a wide range of planting geometry of 1.8 m × 1.8 m to 9 m × 9 m spacing by planting > 3000 trees/ha to < 150 trees/ha. As the growers do not have a defined target wood industry for the produce and thus planting trees in varied stand densities, indicates the lack of optimized space recommendation for *M. dubia* cultivation. As a thumb rule, the collected field data estimates a significant drop in diameter increment with higher stand densities and advancing age (Fig. 6.1). Though, silvicultural practices for *M. dubia* cultivation are evolving slowly based on results of past established woodlots (Warrier 2014, Kirankumar *et al.* 2017) and are yet to define the standard package of production practices.

## 6.4. Tree water requirement and complementarity in resource use

The results of the study indicate that water availability is the main driver of the growth of *M. dubia*. Compared to the effects of water availability, the effects of soil nutrients are appearing smaller. Interestingly, stem wood anatomical traits associated with the water transport capacity reflected the patterns in *AGB* increments (*AGBI*) of *M. Dubia.* At sites with higher water availability, the stem xylem was composed of larger vessel diameters and lower vessel densities. Further, *AGBI* was higher at irrigated sites with a less negative climatological water balance (i.e. with lower rainfall). Hence, results indicate that *M. dubia* benefits from continuous irrigation in the regions that receive annual precipitations substantially below 1,000 mm $yr^{-1}$. The agricultural sector accounts for 70% of the water use in the world (Doungmanee, 2016) and efficient use of the resource is essential for the production of agricultural goods and services, which generate income and create national wealth. Therefore, estimation of tree water requirement, depth of resource access and complementary resource sharing in the *AFS* and mixed plantations are yet to be explored for the species. These scientific insights are required for choice of speciers for agroforestry and plantations and futher to schedule of irrigation and selection of crop combinations.

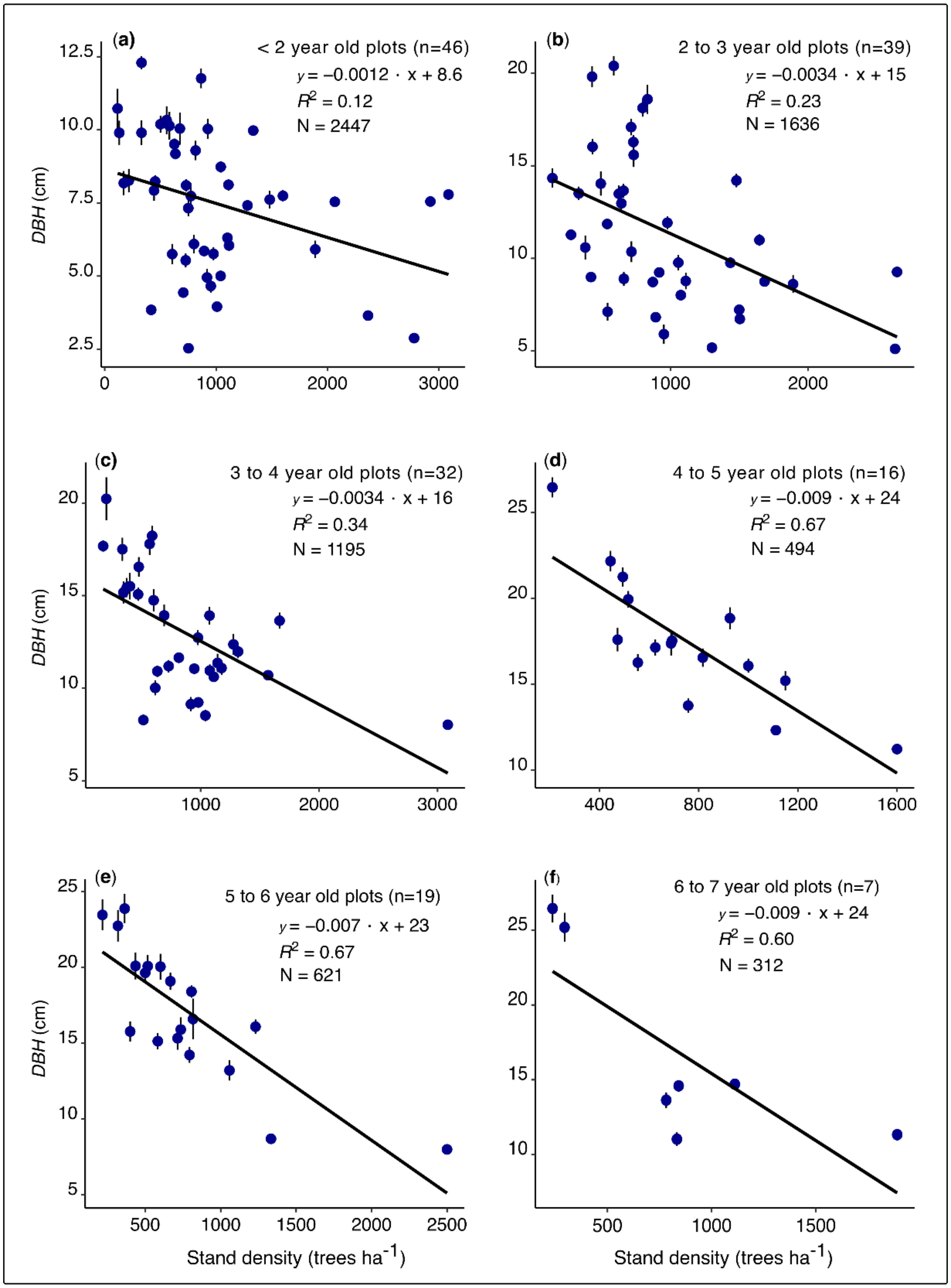


**Fig. 6.1.** The general structure of *M. dubia* agroforestry plantations: very high to low density stands with varying diameter growth. Less influence of stand density on diameter at breast height (*DBH*) growth at younger age of < 2years (**a**) and a significant increase in the influence of stand density over *DBH* in the age group of 2-3 years (**b**), 3-4 years (**c**), 4-5 years (**d**), 5-6 years (**e**) and 6-7 years (**f**) old wood lots. ‘N’ denotes to number of trees enumerated from ‘n’ number of plots.

## 6.5. Soil nutrients and tree growth

Soil nutrient availability is also identifgied as one of the potential factors affect tree productivity (Stape et al., 2010; Campoe et al., 2013; Pérez-Cruzado et al., 2014). The increased availability of nutrients positively impacts average vessel diameter, resulting in higher specific conductivity and increased growth rates (Hacke et al., 2017). Nonetheless, tree hydraulic research frameworks dealing with responses to drought have largely focused on water and carbon associated mechanisms, whereas the role of nutrients is often overlooked (Gessler et al., 2017). The results of the first study indicate that in comparison to the effects of water availability, the effects of available soil nitrogen and phosphorus were 26% to 60% smaller. Whereas, the second study recorded higher *AGBI* at irrigated sites with higher soil phosphorus availability and its effects were also mirrored in larger xylem vessel diameters and lower xylem vessel densities. These results highlight the potential to increase yields in this important short-rotation forest species by improving irrigation and fertilization protocols. Therefore, scopre for studying the nutritional requirement of the *M. dubia* remains wide open for exploring.

## 6.6. *M. dubia* in mixed plantations

Globally, plantation forests are increasing rapidly to reduce deforestation and to avoid the degradation of natural forests, along with provisioning various goods and services (Amazonas et al., 2018; Liu et al., 2018). However, the current trends in plantation forestry advocate for changing from monocultures to more mixed forests for better productivity and biodiversity restoration (Amazonas et al., 2018; Liu et al., 2018; Huang et al., 2018). Agroforestry systems having species mixtures are catching the attention of foresters, smallholders and landowners (Liu et al., 2018). However, there is a relatively limited number of studies on successful species mixtures (Liu et al., 2018). In this context, emerging species like *M. dubia* has to be studied for assessing its performance under mixed stands and complementary resource-sharing capabilities. *M. dubia* is a fast-growing spcies and it can be mixed well with farm forestry agroforestry plantation for ensuring early income to the famers.

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