

Article

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 year⁻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 year⁻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



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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 [1–4]. They are considered particularly important regarding the extent and further expansion of global drylands [5–7]. Fast-growing short-rotation plantations constitute one potentially important component of future climate-smart ‘designer landscapes’ (see, e.g., [8]), 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 [9].

A prime example is India, which houses nearly 18% of the global human population on 2.4% of the world’s land area [10]. Its economic growth and increasing population are associated with an increasing demand for wood and wood-based products [11,12]. In 2019, India imported 8.7 billion USD worth of wood products (Figure S1) [13]. The

further projected high economic growth rate [14], continued population growth [12] and forest policy reforms are expected to create substantial additional demand for wood-based products in the coming years [15]. 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 [16–19]. 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 [20]. There are, however, controversies about potential negative impacts of some introduced plantation species on soil, water and biodiversity [21–23]. This has led to a ban of *Eucalyptus* and *Acacia* plantations in some southern states of India [24].

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 [25,26]. 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 [27,28]. *M. dubia* is a light-demanding, deciduous tree species [29,30] and its wood is suitable for plywood, paper and engineered-wood industries [27,31,32]. 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 [33], 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 [34–38]. 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 [34]. The climatic variable mean annual precipitation often explains a large part of the observed variation in AGB or growth [35,38]; 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 [39,40]. 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 [41–45]. 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 year⁻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.

2. Materials and Methods

2.1. Study Region

The studied woodlots were located in the South Indian states of Andhra Pradesh, Karnataka and Tamil Nadu (Figure 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 year⁻¹

towards the Western Ghats with more than 3000 mm year⁻¹ (Figure 1). Mean annual temperature (MAT) ranges from 29.5 °C in the inland lowlands to 21.6 °C in the highlands (Ghats) [46]. The soils in the region are variable [47] and accommodate diverse vegetation formations ranging from open thorn scrub over wooded grasslands to closed forests [48,49]. 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 [50]. Today, forest cover in the region is about 14% [51].

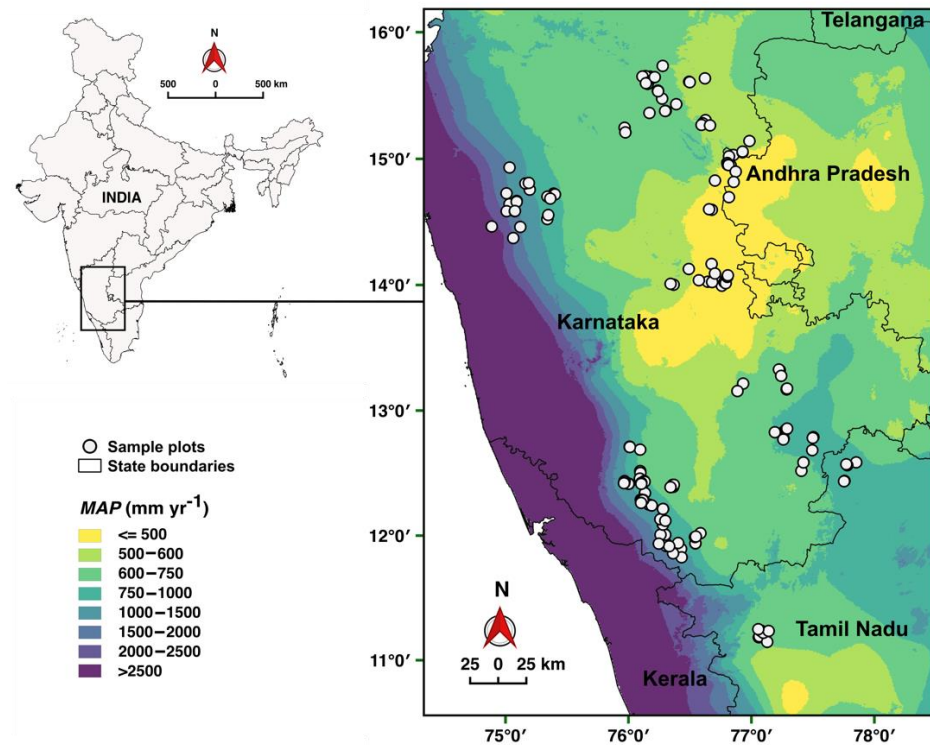


Figure 1. Study region in South India and location of the 186 *M. dubia* woodlots. The sites span across a gradient in mean annual precipitation (MAP) ranging from 420 to 2170 mm year⁻¹.

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 year⁻¹ (Figure 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 [52]). 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.

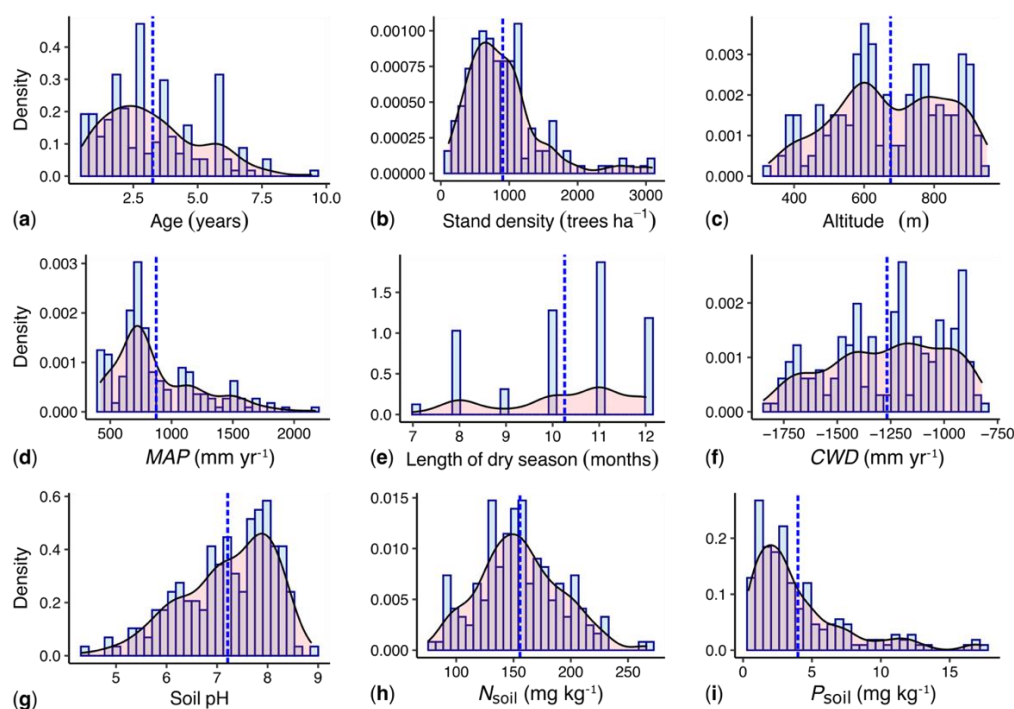


Figure 2. Key characteristics of the studied *M. dubia* woodlots. Histograms and kernel densities of selected key sites and management (a–c), climate (d–f) and soil variables (g–i) along the studied gradients. MAP: Mean annual precipitation; CWD: climatological water deficit; N_{soil} : soil nitrogen content; P_{soil} : soil phosphorous content.

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 year⁻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).

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 m² 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.

2.4. Wood Density

On a subset of 31 woodlots covering a MAP gradient from 420 to 1530 mm year⁻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:

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

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 $0.349 \pm 0.003 \text{ g cm}^{-3}$ (mean \pm 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* [53–55]. WD showed no or only weak correlations ($R < 0.22$) with the available stand, management, climate and soil variables (see overview in Table S1), 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 (Figure S2a–f). We therefore decided to use the overall average of WD for the aboveground biomass estimates at all woodlots in our study.

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 [39], 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* [56–58]. Its pantropical predecessor [59], which yields slightly lower but highly correlated estimates ($R = 1$, Figure S3a), was previously applied for AGB estimation in a *Melia azedarach* plantation [60]. 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 [61], along with mean WD as established in our study, with only marginal divergences from the 1:1 line and close correlation ($R = 1$, Figure S3b). Other potentially suitable equations for tropical trees also produce comparable absolute estimates and close correlations ($n = 6898$ trees, $R > 0.9$, Figure S3c–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 (Figure S2).

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}).

2.6. Bioclimatic Variables

We used the point sampling tool of QGIS software [62] 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 [46]. We further extracted monthly potential evapotranspiration (PET , mm) and aridity index estimates from 30 arc seconds resolution global raster grids [52]. 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. [38], where dry months are defined as months in which PET exceeds precipitation. We further calculated the climatological water deficit (CWD , mm year^{-1}) following Chave et al. [39], 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 [39,40].

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 S1.

2.7. Soil Variables

Soil texture was assessed by the ‘finger probe’ field method [63], 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, Regenstau, 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, CO, 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 [64]. Available soil nitrogen (N_{soil} , mg kg^{-1}) was determined by the alkaline permanganate method [65], available phosphorus (P_{soil} , mg kg^{-1}) by Olsen’s method using ascorbic acid [66] and available potassium (K_{soil} , mg kg^{-1}) was determined with the flame photometer method using ammonium acetate extracts [67]. 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 S1.

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, [68]). Out of the list of more than 40 available stand, management, climate and soil variables (Table S1, Figure S4), 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:

$$AGB_i = a \times age_i^b \quad (3)$$

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

$$\log(AGB_i) = \log(a) + b \times \log(age_i) + \epsilon_i \quad (4)$$

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:

$$a_i = a_0 \times \exp(a_1 \times density_i) \quad (5)$$

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

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:

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

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_{soil} and P_{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 S1).

All statistical analyses and plotting were performed using R (Version 4.0, [69]). We used the open source software Inkscape (Version 1.0, [70]) for aesthetic adjustments on figures.

3. Results

The studied woodlots were vastly heterogeneous with regard to management, climate and soil conditions (Figure 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 ha^{-1} . MAP ranged from 420 to 2170 $mm\ year^{-1}$ and the CWD from -1823 to $-832\ mm\ year^{-1}$. N_{soil} and P_{soil} varied by three- and forty-fold, respectively.

Across all woodlots, stand-level AGB varied from 0.3 to 110.4 $Mg\ ha^{-1}$. 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 ($R = 0.55$, Figure S4). 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 , $p < 0.001$) (Figure 3). It predicted an AGB of 94 $Mg\ ha^{-1}$ for nine-year-old *M. dubia* stands, which corresponded to an average annual AGB increment of 10.4 $Mg\ ha^{-1}\ year^{-1}$.

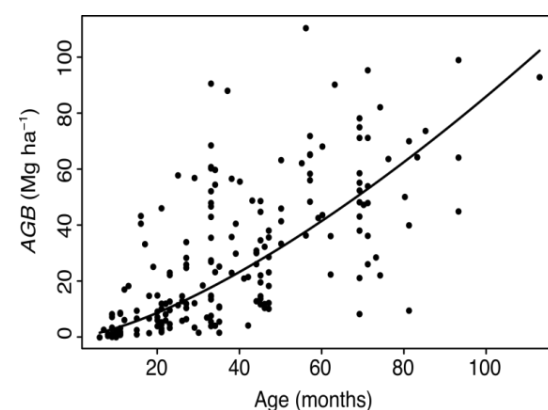


Figure 3. Stand-level aboveground biomass (AGB , $Mg\ ha^{-1}$) vs. stand age (months) across the 186 studied woodlots. The line shows the predictions of a log-log linear regression ($R^2 = 0.55$, F-statistic: 225.4 on 1 and 184 DF , $p < 0.001$). Prediction model: $AGB = 0.12 \times age^{1.42}$, valid 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 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 ($p = 0.173$).

Table 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_{soil} : soil nitrogen content; P_{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: <i>CWD</i>	0.08	0.03	2.62	<0.01
Age: N_{soil}	0.03	0.02	1.62	0.10
Age: P_{soil}	0.05	0.02	2.89	<0.01
Age: <i>CWD</i> : Irrigation (irrigated)	−0.05	0.03	−1.37	0.17

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 (Figure 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 year^{−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 (Figure 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 1).

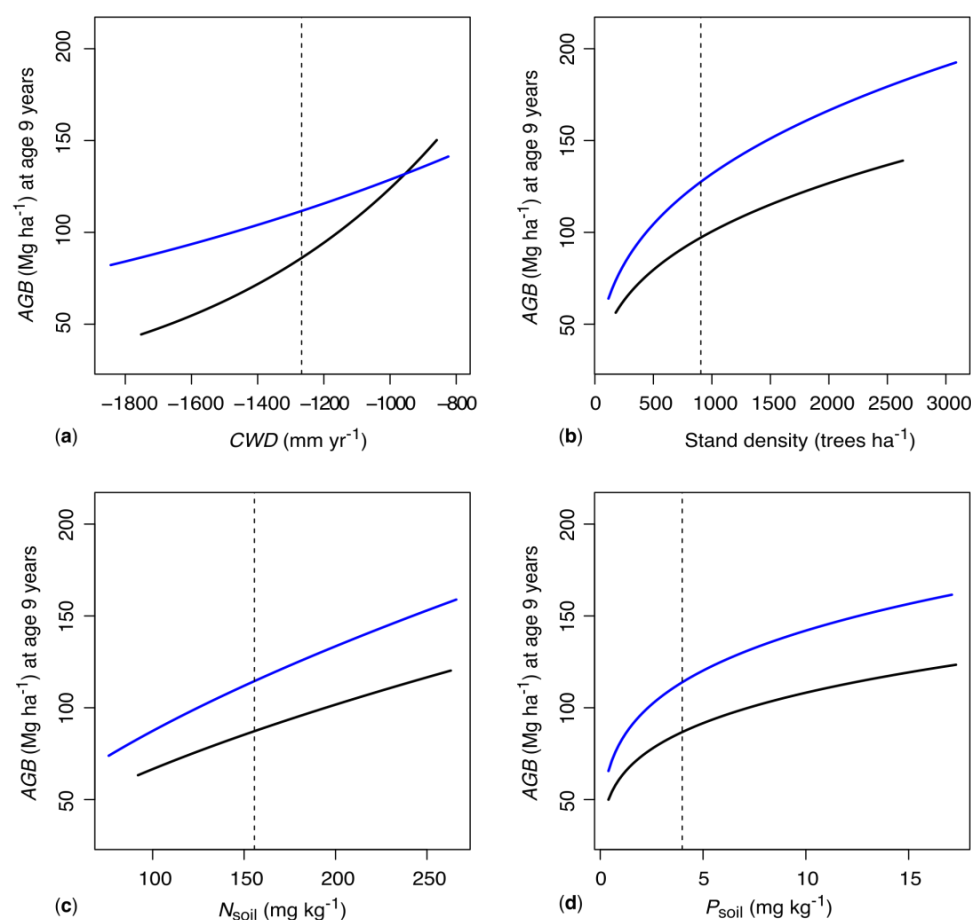


Figure 4. Partial predictions of stand-level aboveground biomass (AGB , $Mg\ ha^{-1}$) of harvest-ready, nine-year-old woodlots as influenced by key management, climate, and soil variables. Along the observed gradients in climatological water deficit (CWD) (a), stand density (b) and soil nitrogen (N_{soil}) (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.

4. Discussion

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 [25,26] (Figure 5). 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 hypothetical 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% [71], 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 $116\ Mg\ ha^{-1}$ [72–74]. 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.



Figure 5. Fully leaved 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).

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 $10.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$. This estimate falls within the range of values reported for four-year-old *M. dubia* plantations in South India (9.6 to $12.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$, estimates derived in analogy to our study using DBH and height data; see Table S2 for details on all cited studies) [33]. 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 $16 \text{ Mg ha}^{-1} \text{ year}^{-1}$, [75,76]), five- to eleven-year-old *Populus deltoides* (6.3 to $16.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$, [77,78]), four- to six-year-old *Gmelina arborea* (0.6 to $8.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$, [79,80]), three- to ten-year-old *Dalbergia sissoo* (2.5 to $7.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$, [41,77,81,82]) as well as from nine-year-old plantations of *Casuarina equisetifolia* ($10.9 \text{ Mg ha}^{-1} \text{ year}^{-1}$), *Pterocarpus marsupium* ($7.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$), *Ailanthus triphysa* ($4.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$) and *Leucaena leucocephala* ($2.6 \text{ Mg ha}^{-1} \text{ year}^{-1}$) [81]. Other studies on common plantation species reported higher AGBI (12.2 to $37.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$, Table S2) than we found for *M. dubia*, both for India [20,44,81,83,84] and other tropical countries [85–88]. 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 $20 \text{ Mg ha}^{-1} \text{ year}^{-1}$ were observed.

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 (Figure 3). Our findings are in line with several previous studies in monocultural short-rotation tree plantations showing similar relationships (e.g., [44,78,89,90]).

The multiple regression model (Table 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 (Figure 4a). The annual CWD was highly significant in the model (Table 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 [34–38].

Likewise, the observed strong positive influence of irrigation of AGB growth is in line with several previous studies in tree plantations [41–44]. 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. $-1000 \text{ mm year}^{-1}$, while an almost twice as high AGB is predicted for irrigated woodlots at the dry end at around $-1800 \text{ mm year}^{-1}$ (Figure 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 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 non-significant in our model (Table 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 ($-1293 \text{ mm year}^{-1}$) 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 (Figure 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}) [33]. 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.

The effect of nutrient availability on *AGB* growth was small compared to the effect of water availability (Table 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 [91,92]. N_{soil} varied three-fold across the studied woodlots, and P_{soil} varied forty-fold. 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 [34,91–93]. 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* (Figure 4d). This suggests that there may be room for further growth optimization by enhanced site selection and by (moderate) fertilizer application on nutrient-poor sites.

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.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/f12121675/s1>: Figure S1: 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 [12,13]. Figure S2: The influence of the key variables stand 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 (gray) 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). Figure S3: Comparison of tree-level aboveground biomass (*AGB*) estimates derived from the pantropical model applied in our study [39] to other *AGB* models. Data from all 6898 studied trees are depicted (dots). The solid blue lines are the respective regression lines, the dashed black lines represent 1:1 lines. Figure S4: Correlation matrix of available growth, climate, soil and management variables. Units and descriptions for all variables are presented in Table S1. Table S1: 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. Table S2: 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. NA: no data available.

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