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Tree or shrub: a functional branch analysis of *Jatropha curcas* L.

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Abstract *Jatropha curcas* is an oil-bearing semi-evergreen shrub or small tree with potential as a source of sustainable biofuel, yet information regarding vegetative and fruit biomass in relation to plant architecture is lacking. Research conducted in Indonesia used the tree based functional branch analysis (FBA) model as a non-destructive method to estimate above and below-ground biomass, and plant architecture. The FBA utility for shrubs was unknown and required modification. This research used destructive measurements to validate modifications to the FBA model that included sub-categorisation of the tapering coefficient for twig, branch, and wood diameter classes, and addition of a fruit load parameter in the distal link. The modified FBA model confirmed jatropha to be a shrub rather than a tree, producing variable estimates for aboveground biomass. This variation was due to morphological plasticity in the length–diameter relationship of the branches that diverged from fractal branching architecture. Fruit biomass variation between replicates was not well estimated and total proximal root diameter was a poor predictor of total root biomass, due to the proximal roots having enlarged water storage structures that do not follow fractal branching assumptions. Jatropha fruit was shown to predominate on twigs with a diameter between 0.9 and 1.4 cm. Understanding the correlation between fruit development and plant architecture will be necessary for fine-tuning the FBA model for future commercial breeding and selection. The high degree of morphological plasticity displayed by jatropha requires consideration when determining plant biomass.

Keywords Aboveground biomass · Allometry · Belowground biomass · Fractal branching architecture · Proximal root · Stem diameter

Introduction

Jatropha curcas L. is a semi-evergreen shrub or small tree with oil-rich seeds, belonging to the *Euphorbiaceae* (Divakara et al. 2010). In Indonesia, there is

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disagreement over whether jatropha is a tree or a crop. Foresters consider jatropha a crop or a plantation crop at best, while agronomists consider it a tree. The disagreement occurs because jatropha has a range of phenotypes; shrub-like, multi-stemmed growth habits with height <5 m, and tree-like, single-stemmed growth habits with height >5 m (Sunil et al. 2013). This problem is not restricted to jatropha as Scheffer et al. (2014) found that 9.2 % of the tree species assessed were classified as shrubs in the TRY (plant traits) database.

Jatropha is of interest for sustainable biofuel production, for socio-economic improvement, and for wasteland reclamation in tropical semiarid regions (Achten et al. 2010; Divakara et al. 2010). Jatropha has been claimed to grow in marginal areas, without competing with food production and is viewed with hopes of providing carbon credits (Divakara et al. 2010; Wani et al. 2012). Many of the envisaged benefits have not materialised. Yields of 12 t ha^{-1} for example have been claimed and global predictions showed yields of only 5 t ha^{-1} (Achten et al. 2014). The problem is that expectations were not based on field performance and validated scientific knowledge (Achten et al. 2014; Edrisi et al. 2015). Although uncertainties remain, knowledge gaps are being filled as is evident by the fact that actual measured yields vary from <0.5–2 t ha^{-1} (Edrisi et al. 2015). However an understanding of jatropha growth and reproductive biology in combination with breeding for available commercial high yielding planting material, optimum management practices, and suitable growing environment are still lacking (Achten et al. 2014; Edrisi et al. 2015).

To capitalise on the commercial potential of jatropha, basic understanding of plant structure, function, and biomass allocation is required. Biomass and fruit production follow from quantitative relationships between plant size and growth (Niklas 1993). Empirical approaches include relationships between dimensional variables such as tree height and stem diameter, leaf area, weight and volume (Lacointe 2000). Allometric equations can be generated from destructive measurements of tree component biomass as dependent variables with easily measured independent variable such as stem diameter at breast height (MacFarlane et al. 2014).

Plant-based models (PBM) (Vos et al. 2010), functional structural plant models (FSPM) (De Reffye et al. 2009), and functional branch analysis (FBA) or fractal branching models (van Noordwijk and Mulia 2002) have been used to quantify growth and biomass. PBMs view plant growth as a function of factors such as light, temperature, nutrients, water and ambient CO_2 and their impact on leaves, stems and roots (Vos et al. 2010). PBMs use defined rules to simulate the physiological process and growth partitions to determine biomass. A limiting factor for PBMs is a lack of feedback between plant growth and plant architecture operating at the phytomer level such as seen in FSPM. In FSPM a phytomer or growing unit (GU) is defined as having one internode, one or more leaves, one or more axillary buds and possibly flowers that form an axis or shoot (De Reffye et al. 2009). FSPM is a virtual plant model based on plant architectural models of Hallé et al. (1978), mathematic models and the Lindenmayer L-system (Prusinkiewicz 2004). FSPM views the plant as a set of phytomers with plant architecture used to integrate environmental responses with feedback between biomass production and biomass partitioning for both development and growth (Vos et al. 2010).

The FBA model (van Noordwijk and Mulia 2002) is a compromise between the PBM and FSPM approaches and uses the “pipe-stem model” theory of fractal geometry of simple tree branching architecture. The pipe model hypothesis is that the cross-sectional area (sum of squared diameters) of branches is equal to that of the preceding stem or branch. FBA models produce equation coefficients that relate aboveground tree biomass to the stem diameter at breast height (DBH) or root biomass to proximal root diameter (van Noordwijk et al. 1994). This eliminates, or at least reduces, the need for destructive sampling to determine biomass. The FBA concept has been used to estimate shoot biomass, root length, and root biomass (Smith 2001; Salas et al. 2004), to estimate tree component biomass using standing tree measurements (Santos Martin et al. 2010), and to derive species-specific and mixed-species biomass equations (MacFarlane et al. 2014). The model does not predict growth, but provides architectural boundary conditions for transport and support tissues to keep up with leaf and fine root development (Mulia et al. 2010).

Jatropha allometric research historically used empirical models and destructive sampling to determine aboveground biomass (Ghezehei et al. 2009; Achten et al. 2010; Makungwa et al. 2013), with limited belowground data (Firdaus and Husni 2012; Baumert and Khamzina 2015). However, there are no data available for biomass partitioning in the generative stage (harvest index). The relationship between inflorescence size, sex ratio, fruit maturation (yield) (Negussie et al. 2014), and plant architecture is important. For instance, in apple and pear trees the reproductive and vegetative branches are different (Costes et al. 2006), while for coffee trees the branches bearing flowers and fruit grow horizontally from the stem (van der Vossen and Herbert 1985; Cilas et al. 2006). In coffee shorter internode length, without a reduction in the numbers of fruit per cluster is also a selection criteria for higher yielding cultivars (Gichimu and Omondi 2010).

FBA has been used to estimate trees biomass but has not been adjusted for shrub architecture. Extension of the plant architectural model to derive potential fruit production has not yet been tested. We therefore set out to test this possibility. The aim of our study was to develop allometric equations for above and belowground jatropha biomass, as grown in Indonesia, using Functional Branch Analysis. Four objectives were: (1) to gain an understanding of the complexity and relationship between jatropha biomass and FBA; (2) to develop improved allometric equations for FBA model in determining above and belowground biomass; (3) to evaluate the FBA model as a non-destructive method for estimating biomass; and (4) to explore whether FBA can be used to identify management practices that increase yield.

Materials and methods

This study was conducted at a jatropha plantation in Mulo Village in the Wonosari District, Gunungkidul Regency of Special Province Yogyakarta in Indonesia (8°0′N, 110°34′E, 185 m ASL). A local company, PT. JGE purchased the land and planted jatropha. No agricultural inputs were applied to the monoculture system and local farmers harvested grass on daily basis for cattle feed, while weeding was performed once a month. Planting material was seed propagated from IP-1M, an improved jatropha population of a first selection from Muktiharjo, Central Java (Hasnam and Hartati 2006). Planting density was 2500 plants ha^{-1}, spaced 2 m × 2 m from seedlings transplanted at 3 months.

The region has an equatorial rainforest climate with mean annual rainfall of 1800 mm, mostly occurring from November to April and months with less than 100 mm per month, mostly in May and October. Mean annual temperature and relative humidity under standard weather station conditions are about 26 °C and 70 % respectively. The soils are Mollisols with texture varying from clay, silty clay to silty clay loam, with poor drainage. Drainage canals were located around the study site to minimise water logging. The soils are shallow, 10–50 cm with limestone beneath. Top soil (0–10 cm) pH (1: 5) was 7.7 with ~0.9 % organic carbon (Walkley–Black method) and total nitrogen (Kjeldahl method), phosphorus (Olsen method), and potassium (ammonium acetate pH 7) were 0.5 mg kg^{-1}, 13.8 mg kg^{-1} and 0.2 cmol$_{(+)}$ kg^{-1} respectively.

Tree selection

This study used jatropha four-year-old jatropha from monoculture plantings. We selected ten unpruned jatropha in good health, with a single-main stem, and with a minimum of 100 branching points (links). Because of the selection criteria, only four trees with fruit were available which affected fruit biomass estimation. Leaf biomass estimation was not affected as the study was performed before leaf fall commenced. At our site, flowering started at the end of October after a light-rain shower and continued until mid June. Fruit harvesting started in mid to late January and continued through to mid August. Leaf flush started at the end of October after the start of rainy season and reached its peak in mid March, while leaf fall started at the end of June and continued to October. For the selected trees, destructive sampling followed the FBA measurement protocol.

FBA measurements

FBA aboveground field measurements started in mid April 2012 and finished at the end of May 2012. FBA belowground field measurements followed and were completed in August 2012. FBA details for field measurements are described in the supplementary material. Biomass calculation using the FBA protocol and workbook are available at http://worldagroforestrycentre.org/regions/southeast_asia/resources/wanulcas/3rd-party-tools/FBA.

Destructive measurements

Aboveground destructive measurements were performed after the FBA aboveground measurements were completed. Each jatropha was harvested to the base of the stem or until the top of root collar was reached. The aboveground biomass was separated into leaves, fruit, twig, branch, and wood or stem categories. Belowground destructive measurements were performed after roots were excavated and the FBA belowground measurements were completed. Roots were harvested and separated into stump plus tap root, fine roots, proximal roots for twig, branch, and wood categories. All the above and belowground biomass separated categories were subject to fresh and dry weight measurements.

Fresh and dry weight measurements

Fresh weights for each aboveground link category, including leaves and fruit were determined. Dry weights were determined for subsamples to generate a dry weight coefficient. All belowground roots for each of the link categories were weighed. No root washing was required as the soil was friable and only needed gentle rubbing with fingers or picking with forceps. Correction factors were necessary for fresh weight of fine roots and roots with twig category for moisture loss during schematic root drawings and measurements due to the time required from drawing to completing fresh weight measurement. The correction factor was determined from other jatropha roots of similar category measured without any delay after harvesting. Dry weight coefficient for above and belowground subsamples was obtained by drying the samples at 70 °C until a constant weight was achieved.

Density measurements

Density measurements for each link category were determined by measuring volume, and wet and dry weights. Volume was measured using single frustum equation (Valdés-Rodríguez et al. 2013). Wet field weights were determined for subsamples of all categories. Dry weights were determined by drying subsamples at 70 °C to a constant weight and applied to the remaining woody parts (Santos Martin et al. 2010).

Leaf and fine root measurements

Average leaf area was determined by sampling 100 leaves from each tree. Leaf area was estimated using allometric equation generated by Pompelli et al. (2012). Specific leaf area (SLA) was determined as leaf area per unit dry weight ($\mathrm{cm}^2\ \mathrm{g}^{-1}$). Leaf dry weight was determined after drying at 70 °C for 24 h. To determine belowground structure required a full root assessment. Fine roots or feeder roots were determined as having a diameter <0.1 cm. Specific root length was total root length per dry weight ($\mathrm{cm\ g}^{-1}$) and determined after drying at 70 °C for 24 h. Average root length was total root length divided by the number of roots.

Tap root biomass estimation

Belowground biomass estimated from FBA does not include biomass of taproot and roots that grew out from the taproot. An empirical biomass equation to fit regression model estimated taproot biomass (Eq. 1):

$$B = aD^b \tag{1}$$

where B is total biomass and D is root diameter while (a) and (b) are the constants. The taproot biomass and diameter data were log-transformed prior to regression analysis using least trimmed squares (LTS) to account for heteroscedasticity and potential outliers in the data. Predicted outputs were back-transformed and verified with a correction factor (Ghezehei et al. 2009). Statistical analysis used SAS 9.3 (SAS Institute Inc., Cary, NC, USA).

FBA validation

Validation of predicted FBA biomass results from biomass of destructive sampling was determined in 1:1 relationship. Because FBA does not use standard fitting techniques, statistical parameters for maximum error (ME), root mean square error (RMSE), coefficient of determination (CD), modelling efficiency (EF), and coefficient of residual mass (CRM) are used (Loague and Green 1991).

Results

Tree parameters

Tree parameters for aboveground biomass determination were generated from 1754 links and belowground biomass derived from 3182 links from ten trees.

Table 1 shows tree parameters for above and belowground with similar and contrasting values. Aboveground branching is an almost perfect bifurcation (2.01) with p and q values closest to the pipe model theory, $p = 1.01$ and $q = 0.66$. The first branching order from the stem shows a sympodial pattern but the next order of branching tends not to be situated opposite each other or following symmetry dichotomous ramification, although it still has a bifurcation of nearly two. Sometimes branches alternate in a herringbone pattern with unequal distances between links, or situated only at one side in an unequal herringbone pattern (Fig. S1).

Average numbers of proximal roots for each tree varied from 7 to 12 with an average diameter of 2.41 cm. This means that proximal roots had double the number of the initial roots. Initially jatropha seedlings propagated from seed show one taproot and four proximal roots that have perpendicular orientation. Over time the initial root structure changes and a more branching structure develops. Mature jatropha also develop 4–8 additional lateral roots that sometimes have oblique roots or lateral roots (sinker roots) that grow vertically similar to the taproot (Reubens et al. 2011).

Compared to aboveground parts, roots had more branches, 2.17 branches at each node and less conservation of cross-sectional area across a branching point ($p = 1.71$, $q = 0.76$; see supplementary material Fig. S2). Distribution of p for belowground values were 61 % skewed toward $p > 1.25$ that were 38 % from the root diameter category corresponding to aboveground branches, 23 % from the 'twig' root category, and 9 % from the 'woody stem' root category. A high p value indicates that the link cross-sectional area before branching was greater than the sum of the cross-sectional area of links after branching. When added to the fact that one branch had a greater cross sectional area (dominant branch) in comparison with the others (q value 0.76), this indicates a herringbone root branching pattern (van Noordwijk et al. 1994). The herringbone pattern for jatropha root had one main axis (mother branch) that started at the base proximal root and branched to form

Table 1 Average (SD) jatropha main branching parameters for FBA model

Parameters	Aboveground		Belowground	
	Average	SD	Average	SD
Diameter of proximal stem (cm)	10.22	2.21	n.a	n.a
Diameter of middle stem (cm)	9.36	2.23	n.a	n.a
Diameter of distal stem (cm)	9.03	2.03	n.a	n.a
Diameter at 2 cm aboveground (cm)	10.10	2.23	n.a	n.a
Number of proximal roots of each tree	n.a	n.a	9.5	2.54
Diameter of proximal roots (cm)	n.a	n.a	2.41	1.17
Number of branches	2.01	0.14	2.17	0.59
p (change in cross sectional area)	1.01	0.61	1.71	1.2
q (relative allocation to largest offspring)	0.66	0.11	0.76	0.15
Twig (D aboveground $\leq$ 1.99 cm; D belowground $<$ 0.5 cm) length (cm)	16.00	14.10	16.21	17.66
Branch (D aboveground = 2–6.99 cm; D belowground = 0.5–1.99 cm) length (cm)	21.98	21.71	20.93	24.08
Wood (D aboveground $\geq$ 7 cm; D belowground $\geq$ 2 cm) length (cm)	11.64	10.59	10.93	11.85
Taper of twig link (cm cm^{-1})	0.05	0.06	0.011	0.0006
Taper of branch link (cm cm^{-1})	0.03	0.1	0.023	0.029
Taper of wood link (cm cm^{-1})	0.10	0.25	0.085	0.14
Twig density (g cm^{-3})	0.30	0.04	0.48	0.22
Branch density (g cm^{-3})	0.32	0.13	0.36	0.23
Wood density (g cm^{-3})	0.34	0.02	0.26	0.12

SD standard deviation, *n.a* not applicable, *D* diameter smaller, daughter branches with fine roots at only one side, and continued for various lengths before branching into almost two equal size sub branches (dichotomous). The daughter branches maintained a similar iteration as the mother branch. According to van Noordwijk and Purnomosidhi (1995) the distribution of q values in a herringbone pattern shows a gradual decrease in value from 1 to 0.5, similar to the pattern shown in Fig. S2.

To apply fractal branching model, mean p and q for above and belowground parameters should have independency with the parent diameter as fractal is scale-independent (van Noordwijk and Mulia 2002). Regression analysis shows R^2 for each parameter is relatively independent and fractal branching model is applicable for jatropha.

The average link length for twig, branch, and wood categories for above and belowground had similar average and standard deviations (Table 1). Average length of twig was 16 cm (SD = 14–17 cm), branch was 21–22 cm (SD = 21–24 cm) and wood was 11–12 cm (SD = 11–12 cm). It seemed for above and belowground link category, increased diameter from twig to branch was followed by increase of length of twig and branch, with the exception of wood category.

Analyses of length and diameter relationship for twig and branch however showed that the relationship was not linear. For this reason, parameterisation of FBA did not use an average value for link length for all categories, but used an average link length for each category. Aboveground final/distal twig links had leaves or leaves and fruit, which means that not all twigs bear fruit. Fruit-bearing twigs were 0.9–1.4 cm in diameter (Fig. 1) with lengths varying from 4 to 65 cm.

Observations, schematic drawings and data from this study and other pruning and no pruning studies in monoculture, intercropping and hedge systems by Tjeuw et al. (2015) showed that approximately 90 % of fruit produced grew on twigs with a vertical to oblique orientation. Twigs with horizontal orientation, especially if the twig originated from water-sprout branches, produced limited quantities of fruit. The majority of water sprout branches that grew horizontally gave rise to lateral twigs that grew vertically and produced fruit. In addition to the growth orientation of fruit-bearing twigs, branching order pattern did not determine the location of fruit-bearing twig. Fruit-bearing twigs were found on the first, second, third, and on higher branching order. Furthermore, multiple number of inflorescences or fruit clusters can occur on the same fruit-bearing twig. For instance, once the first inflorescence has developed and set on the young twig, the twig continues to grow or elongate, producing consecutive inflorescences, while the section where the first inflorescence was initiated develops fruit (Tjeuw et al. 2015).

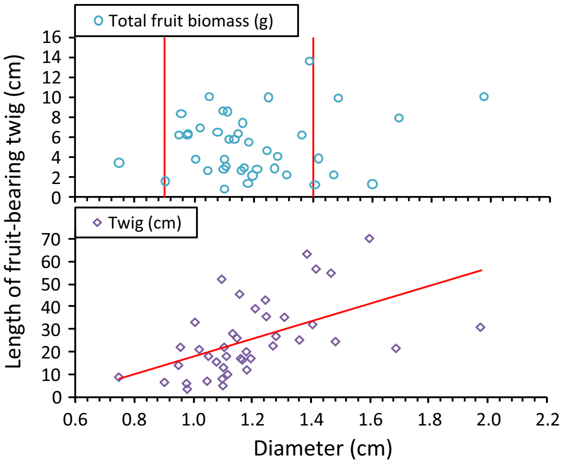


Fig. 1 Relationship between length of fruit-bearing twig with diameter and total fruit biomass; *vertical lines* in-between fruit biomass show *upper* and *lower* limits for diameter boundary determination used for the FBA model; the *sloping line* relating the length of fruit-bearing twig to diameter indicates a proportionality factor

Tapering for above and belowground link of different categories showed a similar pattern with wood having the greatest tapering coefficient compared to branches and twigs, although aboveground wood tapering (0.1) was 18 % greater than belowground wood tapering (0.085). Density for aboveground twig, branch, and wood was around 0.3 g cm^{-1} although wood had the greatest density at 0.34 g cm^{-1}. The aboveground density values are very close to the density values determined for 4 month old jatropha seedlings by Achten et al. (2010), 0.2 g cm^{-1} (SD = 0.01) for stem and 0.26 g cm^{-1} (SD = 0.03) for wood parts. On the contrary, density of wood for the belowground category had a lesser density 0.26 g cm^{-1} compared with the branch (0.36 g cm^{-1}) and twig (0.48 g cm^{-1}). Mujumdar et al. (2000) and Krishnamurthy et al. (2012) found jatropha roots had a well-defined cortex of which large parenchymatous cells arranged centripetally that were mostly for water storage and had xylem vessels with assorted sizes, but did not have xylem fibres. The absence of xylem fibres explains the light wood characteristic of jatropha.

Adjustments to the FBA model

As data showed that a single tapering coefficient was insufficient, three separate tapering coefficients for twig, branch, and wood were introduced. Estimates for fruit biomass were also included, based on distance between fruit on twigs of specified diameter.

FBA output and allometric equations

Figure 2 shows the predicted increase of above and belowground biomass with increased ratio of proximal root diameter to stem base diameter. The increase in total aboveground weight was much greater than total proximal root weight. For total aboveground weight, branch category made the biggest contribution to total aboveground weight followed by twig and leaf, and finally by fruit. The data serves as the basis for construction of allometric equations (Table 2).

The scaling coefficients derived for total aboveground biomass (2.58) were greater than proximal root biomass (2.12). Twig and leaf biomass scaling was similar to fruit biomass. This is because twigs bear leaves and fruit.

FBA for belowground only simulates proximal root biomass, and not the remaining root biomass such as the taproot and other roots that originate from the taproot. For this reason, the scaling coefficient for the remaining roots required the use of an empirical allometric power equation with regression analysis. Analysis using least trimmed squares (LTS) regression gave an allometric constant (*a*) of 0.018 and scaling coefficient (*b*) of 1.33 ($p > 0.0001$). See Table S1 for details.

Table 2 FBA allometric constants and scaling coefficients ($B = aD^b$) for above and belowground biomass

FBA scaling coefficients	*a*	*b*
Aboveground		
Total biomass	0.0090	2.5825
Branch biomass	0.0088	2.2666
Twig & leaf biomass	0.0085	2.1209
Fruit biomass	0.0004	2.1127
Belowground		
Proximal root biomass	0.0097	2.1870

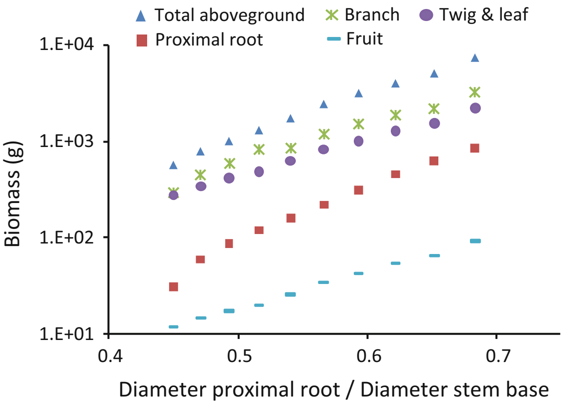
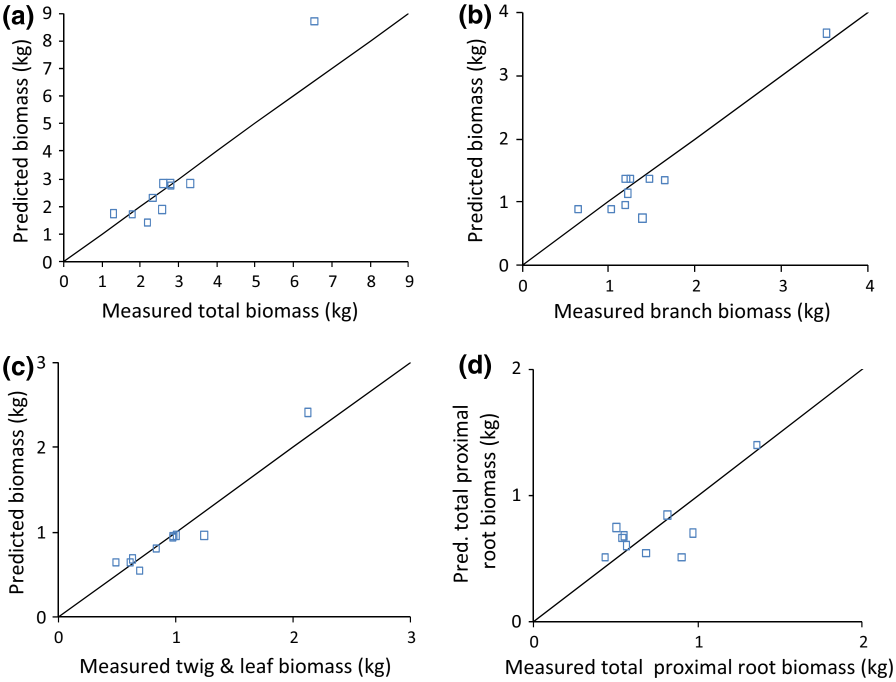


Fig. 2 Relationship of biomass and ratio diameter of proximal root to stem base from FBA output

FBA validation

Figure 3 shows a direct comparison around a 1:1 line for FBA predicted and measured values derived from destructive measurements. The FBA model was able to predict total aboveground biomass, branch biomass, and twig and leaf biomass for all jatropha except one. This exception had a much larger basal diameter and was outside the FBA range for the other samples. This outlier was retained within the analysis based on statistical advice as it provides a more realistic representation of the phenotypic or morphological plasticity (heterogeneity) that currently exists with the planting material. Until more uniform planting material can be developed through intensive breeding and selection, the high levels of heterogeneity will require careful statistical consideration. The residuals between measured and predicted (FBA model) for total aboveground jatropha biomass showed significant negative correlation with tree height ($R^2 = 0.89$; $p = 0.015$), crown length ($R^2 = 0.91$; $p = 0.013$) and width ($R^2 = 0.89$; $p = 0.019$). This resulted in a short crown being predicted as having a massive crown, while a long crown was predicted as having a small crown. Similar to crown length, a narrow crown was predicted as having a wide crown, while a wider crown was predicted as having a narrower crown. FBA for tree height was generated by adding crown length and length of stem/trunk, therefore bias in crown length resulted in bias in tree height as well.

Fig. 3 Comparison of predicted and measured aboveground tree biomass components: **a** measured total biomass, **b** measured branch biomass, **c** measured twig and leaf biomass and for belowground **d** measured total proximal root biomass



Comparison of predicted and measured belowground biomass shows the model is able to predict total proximal biomass for total proximal root of some trees, but over-estimated small proximal roots in some, and under-estimated large proximal roots in others. Unlike links for the aboveground, the proximal root link for belowground had a different size, shape and length, especially for diameter of branch and wood category links.

Overall, statistical analysis for total aboveground biomass, branch biomass, and twig and leaf biomass indicate the model has an acceptable prediction range and is applicable for biomass estimation (Table 3). Statistical analysis of fruit biomass was not able to confirm viability of the FBA model. Fruit data were limited with only four of the ten trees having fruit. FBA generates fruit biomass based on fruit bearing twig diameter and information relating to this link was limited.

Statistical analysis of total proximal root biomass for belowground showed that the proximal root diameter used in the FBA model only accounts for 56 % ($R^2 = 0.56$) of the total proximal root biomass. The remaining percentage was attributable to other, unknown variable(s).

Predictors for aboveground biomass

According to FBA model, above and belowground branching is interconnected and subject to the same rules, therefore stem base diameters relate to root collar diameter and sum of squared diameter proximal roots. Using these independent variables to predict aboveground total biomass of the ten sample trees, the result shows that stem base diameter is the best predictor; followed by square root of sum squared diameter proximal root, root collar diameter and number of proximal root (Fig. 4). RMSE for stem base diameter is 27.9, square root of sum squared diameter proximal root is 37.5, root collar diameter is 50.1, and number of proximal root is 56.6. The sum of squared diameter proximal root overestimates aboveground biomass because the diameters include the structures that function as water storage units.

Comparison with other jatropha allometric equations

Empirical allometric equations are available for jatropha biomass from other studies (Table 4). Achten et al. (2010) developed empirical allometric equations

Table 3 Statistical validation of FBA model for above and belowground biomass estimation

Parameter	Optimum & range values	Aboveground biomass				Belowground biomass
		Total	Branch	Twig & leaf	Fruit	Total proximal root
R^2	(1, ≥0)	0.93	0.90	0.92	0.05	0.56
Maximum error (ME)	(0, ≥0)	2.16	0.64	0.29	0.04	0.39
Root mean square error (RMSE)	(0, ≥0)	27.86	18.49	15.33	62.80	25.36
Modelling efficiency (EF)	(1, ≤1)	0.66	0.86	0.89	−0.06	0.52
Coefficient of residual mass (CRM)	(0, ≤1)	−0.03	0.06	0.003	0.19	0.02
Coefficient of determination (CD)	(1, ≥0)	0.46	0.83	0.76	5.75	1.17

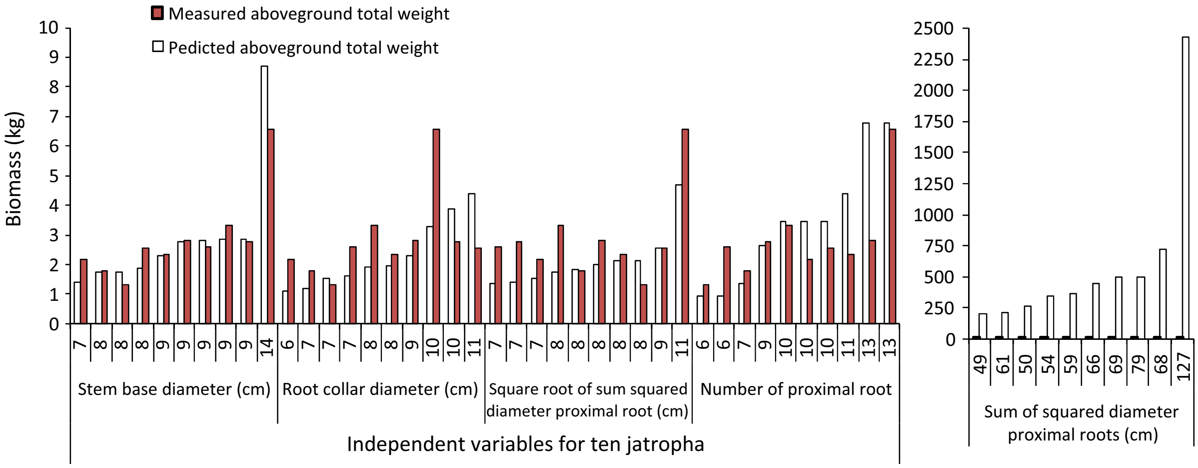


Fig. 4 Biomass of measured and predicted aboveground total weight generated from several independent variables using FBA allometric coefficients in ten trees

using stem diameter to estimate aboveground biomass based on data obtained from 41 jatropha seedlings (up to 3 cm stem diameter), while Ghezehei et al. (2009) used stem base diameter and other predictors to develop allometric equations for aboveground biomass estimation using 12 samples aged 16–24-month-old. Makungwa et al. (2013) developed two aboveground biomass allometric equations based on stem diameter measured at 10 cm aboveground from 172 and 442 samples of one to three-year-old jatropha planted as smallholder crop boundary hedges, in five different regions. Firdaus and Husni (2012) determined allometric equations for aboveground and belowground biomass using stem diameter from 15 sampling of 6–46-month-old jatropha. Baumert and Khamzina (2015) developed above and belowground biomass allometric equations using stem diameter measured at 20 cm from aboveground. The allometric equations were classified as juvenile, adult, and mature based on stem diameter grouping. Data were collected from 141-jatropha plants aged 1–20 years, taken from various production systems.

In Fig. 5 we present the intercept (*a*) and power coefficient (*b*) relationships for jatropha allometric equations from six authors, including our jatropha FBA. While the result shows a strong *a* and *b* relationship with only one degree of freedom it does not indicate any biological association. It does however suggest that for a particular value of *a*, only a limited range of values for *b* might be exist, irrespective of any factors (Hairiah et al. 2011). In essence, this allows us to simplify matters and develop one jatropha biomass/diameter allometric equation.

Despite the apparent differences in parameters, a comparison of total aboveground jatropha biomass in relation to stem base or stem diameter showed similar

Table 4 Jatropha allometric equations from several sources

Allometric scaling coefficients	Number of sample	*a*	*b*
Aboveground			
Achten et al. (2010)	41	0.029000	2.328
Ghezehei et al. (2009)	12	0.000907	3.354
Makungwa et al. (2013) 1st equation	172	0.006700	2.891
Makungwa et al. (2013) 2nd equation	442	0.005500	2.769
Firdaus and Husni (2012)	15	0.002330	3.320
Baumert and Khamzina (2015) juvenile stage		0.003000	2.740
Baumert and Khamzina (2015) adult stage	141	0.003000	3.030
Baumert and Khamzina (2015) mature stage		0.016000	2.310
Belowground			
Firdaus and Husni (2012)	15	0.000880	3.110
Baumert and Khamzina (2015) juvenile stage		0.001000	2.710
Baumert and Khamzina (2015) adult stage	141	0.001000	2.920
Baumert and Khamzina (2015) mature stage		0.016000	1.880

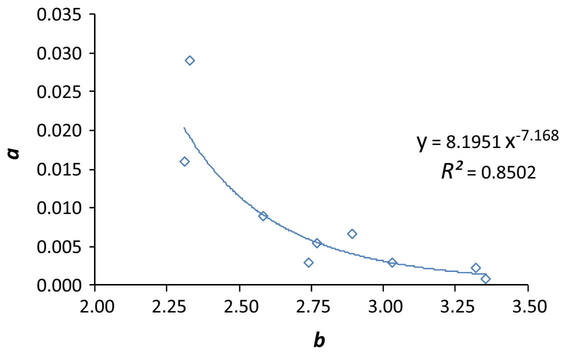


Fig. 5 Relationship of intercept (*a*) and power coefficient (*b*) from allometric equations for jatropha from several sources

trends between published sources and the FBA results (Fig. 6). Achten et al. (2010), the first equation of Makungwa et al. (2013) and Firdaus and Husni (2012) share similar patterns with the highest aboveground biomass estimations, whereas Ghezehei et al. (2009) and juvenile stage of Baumert and Khamzina (2015) share the lowest aboveground biomass estimations. The second equation of Makungwa et al. (2013), jatropha FBA, adult and mature stage of Baumert and Khamzina (2015) are situated in the middle of previous two patterns. The grouping pattern for increasing biomass with increasing diameter is likely due to similarities in age. Moreover variations in jatropha biomass across different sources derived from empirical allometric and jatropha FBA can be caused by differences in planting material, site characteristics such as soil, vegetation and over-storey structure (MacFarlane et al. 2014), or in silvicultural practices and development stage or age at the time data were collected (Ghezehei et al. 2009; Makungwa et al. 2013).

As further explored in ongoing research for allometric equations of other species (Harja, pers. comm.), a reformulation of the allometric model to $Y_x = \left(\frac{D}{x}\right)^b$, with a reference diameter (x) of in this case about 14 cm, can maximise statistical independence of the modified a (Y_x) and the b parameter for all jatropha results (Table 4 plus our study). The FBA result for $Y(14)$ is 15 % lower than the mean of the previous studies.

Ratio below to aboveground biomass

The ratio of belowground to aboveground biomass or root to shoot ratio (R/S) is a widely used measure to estimate belowground biomass as it is much easier to measure biomass aboveground than belowground. The ratio between belowground to aboveground biomass for this study was determined at 0.5; SD = 0.13. The aboveground biomass explained 83 % ($R^2 = 0.83$) of the variation in the belowground biomass (Fig. 7).

The majority of the below to aboveground ratios were concentrated at the lower end of the regression line with one outlier located at the opposite end. This is because one tree had a much greater below and aboveground biomass in comparison to the remaining trees. The relationship between above and

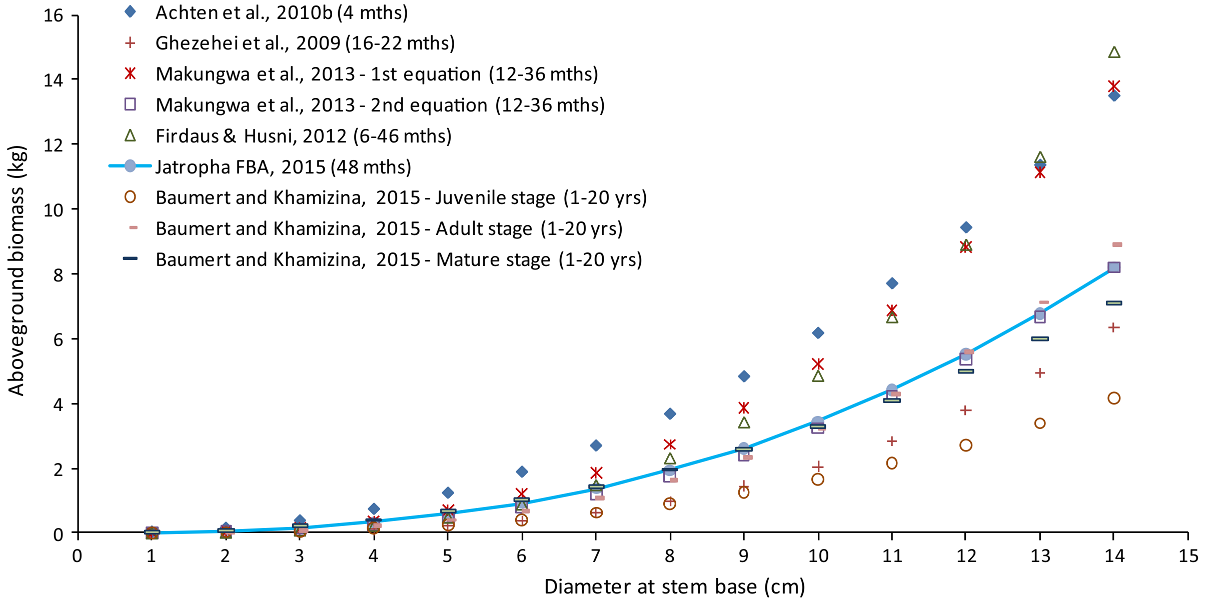


Fig. 6 Relationship of aboveground biomass and diameter at stem base using different jatropha allometric equations from several sources

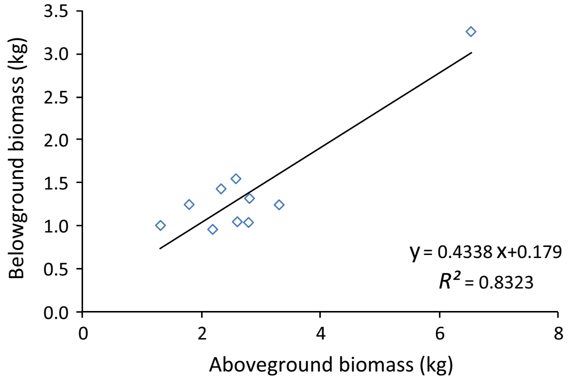


Fig. 7 Relationship between belowground and aboveground biomass

belowground biomass could be explained by the fact that root biomass is essentially the extension of stem underground and branches into taproot and proximal roots, in agreement with the pipe-stem model theory.

Firdaus and Husni (2012) using destructive sampling determined the below to aboveground ratio to be 0.4 for seedlings aged 6–46 months in wasteland areas in Malaysia. Rao et al. (2013) also using destructive sampling, found the below to aboveground ratio to be around 0.3 for jatropha trees aged 8 years in Southern India. Wani et al. (2012) used a below to aboveground ratio of 0.2 to factor the belowground biomass for trees aged 3–5 years in Northern and Southern parts of India. Use of a 0.2 ratio clearly underestimated belowground biomass compared with empirical data. Differences in the below to aboveground ratio results can be due to planting material and tree age, also the agro-ecological conditions of soil, climate and management practises, but also measurement methods, especially for belowground biomass (Mokany et al. 2006; Kuyah et al. 2012).

Discussion

The FBA model produces both good and poor aboveground biomass estimates of jatropha. This is dependent on how well the jatropha fits the fractal-like allometric scaling dimensions. The poor estimation of aboveground biomass results from inconsistencies in the bias for crown length and width, and tree height estimations. FBA generates crown length by summing the length of links specified by length-diameter relationships. The way link length relates to link diameter is a key relationship in the FBA model calculations. Our data for twig, branch, and wood links did not linearly relate to link diameter and showed a wide variation between trees (Fig. S3), with the exception of twigs bearing fruit (Fig. 1). In the absence of such relationship, FBA uses a single value for mean and variance, independent of diameter. Biologically, this relationship is complex as link length is determined by the development and disappearance (self-pruning) of branches, in the axes of (former) leaves. Enhanced development of side branches at the crown surface leads to shortening of link lengths, while shading of the lower branches leads to senescence of side branches (Mäkelä and Valentine 2006) and secondary elongation of links as measured in the FBA protocol. Such trees can be thought of as 'disrupted fractals' where the lengths of links of different diameter branches are somewhat randomised due to historical branch development that effects link length (MacFarlane et al. 2014). This may explain why further statistical approaches using mean link length and measured variability were sufficient to reconstruct measured biomass for some, but were still insufficient to predict biomass for others. Although, this technique provides more structure (predictability) in the location of shorter and longer links in the crown than FBA uses, it cannot fully capture the wide variation between tree links.

Jatropha in this study showed sympodial growth, some with dichasia, and others with multiple branching. The branching pattern follows Leeuwenberg's model (Hallé et al. 1978). Other branching patterns are possible due to the high phenotypic plasticity. Sunil et al. (2013) observed several branching habits and patterns between different germplasm in a monoculture planting at 2 m × 2 m, with no pruning, and receiving similar management treatments. Although aboveground phenotypes show a wide range of plasticity, genetic diversity is narrow (Divakara et al. 2010).

The FBA model generates the crown radius allometric coefficients using a vertical projection of the crown leaf area and assuming the shape is uniformly circular. This assumption does not hold for all jatropha so wide crowns may be underestimated while narrow crowns, overestimated. Jatropha grown in a plantation environment may not develop crowns that reach their full potential as they compete within a limited growing space for light, soil nutrient, and water (Mäkelä and Albrektson 1992; Martin et al. 2012). For instance, competition for light between trees may result in shoot or tree crown clumping or self-pruning (Duursma and Mäkelä 2007). Adding to the complexity of competition is the fact that the jatropha used in the FBA calculations showed substantial phenotypic plasticity. This is despite the fact that the planting material is from one improved population. Future biomass prediction with FBA model may benefit from stratified sampling based on different diameter classes, crown size and shape.

FBA calculates tree height by adding trunk/stem length with fractal crown length. The source of tree height bias for some jatropha came from the crown length bias, as there was no significant correlation between residuals of FBA stem height and measured stem height. Jatropha stem lengths used in this study varied from 2 to 40 cm from soil surface therefore diameter at breast height (DBH) normally used for developing tree allometric equation was replaced with stem base diameter measured at the middle of the stem length. Moreover, jatropha used in this study was only four-year-old and had stem base diameter ranging from 7 to 14 cm therefore a reduction in the wood link diameter categorisation to ≥ 7 cm was required. Consequently, data for wood and main stem parameterisation were identical. The strong tapering found for the main stem did not apply to the branches, therefore the FBA model was adjusted to use separate tapering coefficients for twigs, branches, and wood. The tapering coefficient interacts with the proportionality factor p of cross-sectional area before and after a branching point, in determining the cross-sectional area before the next branching point. When this aboveground structure is considered, jatropha approximates a shrub more than a tree.

FBA for forest trees construct a biomass for the crown wood, branches, twig and leaf, and add the trunk biomass separately as it is subject to other biological and management-related processes. Fractal (self-similarity) properties of the branches are restricted to the crown (Mäkelä 2002; Mäkelä and Valentine 2006). Similar to FBA for forest tree, jatropha biomass was constructed in the same way, with addition of fruit biomass.

The FBA model also using parameters for fruit-bearing twigs predicted an allometric scaling coefficient (b) of 2.11 for fruit biomass relative to the stem base diameter. This is in agreement with a value of <2.2 for the allometric scaling coefficient for plant reproductive biomass when the stem tapered (Niklas 1993). Although the predicted scaling coefficient for fruit biomass is in agreement with other studies, the fruit data for this study was limited and results for older plants may differ.

Corner's rule recognises a positive correlation between twig size and leaf, inflorescence, fruit, and seed size (Westoby and Wright 2003; Chen et al. 2010). For fruit-bearing twigs in jatropha, twig length and diameter were correlated; twig diameter was better as predictor of fruit presence than link length, with twig diameters between 0.9 and 1.4 cm representing 83 % of fruits observed. Chen et al. (2009) studied fruit-bearing twigs across 55 woody species and found that fruit and seed biomass were positively correlated with twig diameter, but negatively correlated with the ratio of twig length to diameter. Chen et al. (2009) also found that twig size was not significantly correlated with seed size, possibly due to the large variation in seed numbers per fruit and a negative relationship between seed size and number of seeds per fruit.

Although the study of fruit-bearing twigs in relation to reproductive biomass is still in the very early stages, this study highlights the importance of architecture, especially when trying to correlate fruit biomass with breeding and management practices. Research into the relationships between length and diameter for links bearing fruit, fruit dimensions, and pericarp to seed ratios is required for improved simulations. It will also be important to investigate the critical switching point for twigs with diameters between 0.9 and 1.4 cm to understand why some twigs bear inflorescences and others do not. Moreover, fruit-bearing twigs can be located anywhere on the tree regardless of the branching order and often bear multiple inflorescences or fruit clusters (Tjeuw et al. 2015). Contrary to the observations by Ghosh et al. (2011) our results show that branches situated in the lower part of the canopy and shaded by upper branches do flower and produce fruit, although at a reduced level. If light does determine flowering, then there must be a range over which it operates given that inflorescence initiation and fruit set occurs in areas where light is limited. Such a range is likely influenced by resource availability and allocation in combination with twig diameter. This possibility opens up an interesting area of research into flowering physiology in response to twig size and external stimuli such as light quality and/or quantity.

It is important for plant breeders to understand age-related characteristics to be able to optimise genetic gains per unit of time, rather than waiting for a tree to start producing. An example of this is coffee breeding where yield prediction is possible through architectural development, as coffee only flowers and fruits on lignified plagiotropic (horizontal) branches (Cilas et al. 2006). In coffee, the internode length between inflorescences on plagiotropic branches is an important trait, as it not only determines carbohydrate allocation, but also carbohydrate distribution to inflorescences and fruit. Based on understanding of coffee tree architecture, selective branch pruning, branch-wounding (ring-barking) and grafting of productive plagiotropic branches to other trees to increase yields is already standard management practice (Esther and Adomako 2010). Plant architecture has proved commercially beneficial in coffee breeding and may prove useful for future jatropha breeding and management practices.

FBA belowground biomass estimation for total proximal root biomass had a greater bias compared with aboveground biomass. Proximal roots enlarge into structures that store water, a root structure not factored into the FBA pipe model theory. The theory determines that a pipe represents a 'bundle of unit pipes' each of which has a water and nutrient transport function (Mäkelä 1986). The bundles of pipes are interconnected, one to the other where transport capacity is determined by the stem or proximal diameter (van Noordwijk and Purnomosidhi 1995).

FBA belowground biomass estimations do not take into account taproot or stump biomass, as these organs do not follow a fractal model; these organs, however contribute 30 % of total measured belowground biomass in jatropha. For this reason, it is necessary to generate empirical allometric equations for the taproot using its diameter as the predictor variable. The estimated taproot weight can be added to estimated total biomass based on proximal roots as a predictor, to derive total belowground biomass.

Jatropha roots typically are intermediate in branching pattern between a herringbone and dichotomy pattern (van Noordwijk et al. 1994). Herringbone root systems minimise intra-plant root competition so are more effective at resource acquisition, despite their roots being larger, and more resource demanding. Dichotomous root systems have higher intra-plant competition although they are smaller and require less resources (Fitter et al. 1991). It is apparent that jatropha is able to respond to differences in resources availability through root structure modification.

Implementation of the revised FBA model (with tapering coefficients depending on link diameter classes) for estimating jatropha biomass will be easier and cheaper than relying on destructive methods for further studies. For density measurements a small tree corer could be used to extract a sample, alternatively using previously published density values (MacFarlane et al. 2014). The revised FBA model offers estimations of biomass partitioning for fruit, twig and leaf, and branch, including total biomass. FBA also shows that aboveground fractals are interconnected with belowground fractals, and that root collar diameter and square root of sum squared proximal root diameter can be used to estimate aboveground biomass. The best estimation for aboveground biomass however comes from using stem base diameter.

Below to aboveground ratio is a function of genotype and a reflection of resource allocation and the limitations (stress) imposed within the environment (Taub and Goldberg 1996; Aikio and Markkola 2002). Although not fully understood, above and belowground parts are functionally interdependent and able to maintain a dynamic biomass balance depending on resource availability. In basic terms when light is the predominant limiting factor, resources are allocated to aboveground growth, and when nutrients are the limiting factor, preference is given to belowground growth. Jatropha is a shade intolerant plant therefore a greater proportion of biomass is invested aboveground than belowground. In this study light was probably a limiting factor as canopy closure had already occurred in the four-year-old jatropha planted at 2 m × 2 m. The below to aboveground ratio is an indicator of functional plasticity (Aikio and Markkola 2002) in response to growth-limiting resources. In jatropha the roots act as belowground storage organ as part of overall plastic response (Grams and Andersen 2007).

Conclusions

From the FBA perspective, *Jatropha curcas* is categorised as a shrub more than a tree as it does not have a prominent trunk. Implementation of a revised FBA model provides variable estimations of total aboveground biomass for twig, leaf and branch biomass depending on how well the jatropha fit the fractal branching architecture. The strength of this model is its application as a non-destructive technique for determining aboveground biomass. Fruit biomass was not well estimated so further research is required on fruit-bearing twigs and fruit dimensions to fine-tune the model. Proximal roots as a predictor of belowground biomass produced poor results because the cross sectional area of the proximal root do not follow the fractal branching pattern. One possible solution might be to use root diameters farther from the stem as basis for allometric equations. The measured below to aboveground ratio of 0.5 observed in this research was higher than in other jatropha studies. These differences highlight a degree of morphological plasticity that requires consideration when determining plant biomass. Below to aboveground ratio requires referencing against whole plant biomass for meaningful results.

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