



Investigations of on farm seedling productivity of the rare and declining *Caesalpinia bonduc* in Benin (West Africa) by aid of simulation modelling

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Abstract

Caesalpinia bonduc is overexploited and threatened due to its importance in medicine. This study aims at assessing on farm seedling productivity of *C. bonduc* by aid of simulation modelling in order to design its appropriate plantation techniques, harvesting intervals, and soil conditions. Data were collected from nursery and field experiments by measuring stem height, collar diameter, number of leaves and tap root length during 180 days. The simulation model was based on a metabolic pool type model calibrated first to simulate the observed growth data from the nursery (calibration). Following it was used to simulate the growth of plants from field experiments, first by an optimization of the utilization of leaves or roots only, and second by an optimization of the utilization of both leaves and roots at the same time at different plant densities and nitrogen levels. The models show that in order to optimize the utilization of *C. bonduc* it should be planted at high densities with high nitrogen levels. Leaves and roots harvesting should take place every 50-60 days, and maximum 15% of the biomass of roots and leaves should be harvested at each harvesting event.

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Introduction

Information on optimal planting densities, harvesting intervals and soil conditions are important in order to design appropriate plantation techniques and sustainable harvesting practices. As it can be very laborious and time consuming to investigate a long list of different growing and utilization strategies (initiation time, frequency, intensity) under various climatic conditions and soil nutrient levels, especially when talking about woody species where growth to maturity takes several years, simulation modelling is an attractive alternative to long term experiments (Emanuel *et al.*, 2005; Pandey and Bhargava, 2014). It will not be possible to use any kind of model for plant growth, as the model must be detailed enough to capture the biological reactions of the plants to utilization of different organs such as leaves, branches and roots. A simulation model with the appropriate detail level has been described by Gutierrez (1996), and a metabolic pool simulation model has been developed further for instance by Sønderskov *et al.* (2006) to include competition between several plant species for light and nitrogen, and by Rodriguez *et al.* (2011) and Ponti *et al.* (2013) to include the growth of woody crops such as coffee and olive. Further modifications of the metabolic pool simulation model by Sønderskov *et al.* (2006) are, however, necessary in order to make the models realistic and functional for modelling growth of woody plants in African natural environments.

Few long term data are available from Africa, but suitable data were found to develop the models based on growth data of one shrub species, *Caesalpinia bonduc* L. *Caesalpinia bonduc* is a thorny shrub widely distributed throughout the tropical and subtropical regions of the world (Kapoor, 2005). It is an important medicinal plant, where mainly roots, but also leaves and seeds are exploited. It is considered the most commercialized medicinal species in the southern part of Benin (Vodouhê *et al.*, 2008). *C. bonduc* is classified as rare and endangered (Harden, 2002), and in Benin it has been reported extinct in the wild, although the species can be found in home gardens from the Guinean to the Sudanian

zone (Adomou, 2005; Assogbadjo *et al.*, 2012). In Africa, the long-term viability of *C. bonduc* subpopulations is threatened by overexploitation of its roots (Hutton, 2001). Furthermore, there is a low genetic diversity within the species, which may imply high risks for future extinction (Assogbadjo *et al.*, 2012). Local people have traditionally used unsustainable methods to extract roots, leaves and seeds of *C. bonduc*; for example by harvesting the branches in order to stimulate the development of roots. Presently local people have developed different strategies to domesticate the species on farms for commercialization and in home gardens for local medicinal use (Assogbadjo *et al.*, 2011).

In order to exploit *C. bonduc* optimally as a farming crop, knowledge on appropriate utilization strategies are needed, for instance planting and breeding techniques. Seed germination of the species is influenced by seed scarification (Hessou *et al.*, 2009) instead of seed morphology (under review). However the seedling and plant growth are influence by seed morphology and the large seeds are superior in terms of seedling and plant growth (under review). The vegetative propagation of the species has been found to be efficient using hormonally treated stem cuttings (Tiwari *et al.*, 2010) and root explants (Santosh Kumar *et al.*, 2012).

Information on optimal planting densities, harvesting intervals and soil conditions are also important in order to design appropriate plantation techniques and harvesting practices. In the present study a metabolic pool simulation model developed by Sønderskov *et al.* (2006) was modified to be able to simulate the growth of trees and was used to come up with suggestions on how to optimize the utilization of *C. bonduc* on the short term, i.e. up to 3½ years. The aim was to estimate both how frequently roots and leaves can be harvested and which percentages can be harvested each time to optimize the yield.

Materials and methods

Caesalpinia bonduc is a thorny shrub with large bipinnate leaves. Its flowers are yellow and fruits are

inflated pods with 1-2 seeds (Prajapati *et al.*, 2006). In traditional medicine different parts of the plant are used to treat asthma, chronic fever, cough, headache and stomach upset (Nandkarni, 1976; Satyavati *et al.*, 1956; Chopra *et al.*, 1956). Twenty properties from the leaves, roots and seeds of the species are used by the local populations in Benin to ease childbirth, to treat burns and for cultural practices like games, weddings and the Fâ ritual (Assogbadjo *et al.*, 2012). Different parts of the plant have shown a variety of pharmacological activities such as antimicrobial, adaptogenic, contractile activity in smooth muscles and skeletal muscles and antifilarial activity (Simin *et al.*, 2001; Kannur *et al.*, 2006; Datté *et al.*, 2004; Rastogi *et al.*, 1996). The plant is proved antiinflammatory (Jethmalani *et al.*, 1966), anthelmintic and antimalarial (Jain *et al.*, 1992). It is an aphrodisiac and a general tonic helping in the rejuvenation of the body (Shrikantha Murthy, 2000). The exploitation of the species leads to overexploitation and threatens the species in Benin.

Planting experiments

A nursery experiment was carried out in January 2010 at the University of Abomey-Calavi, Benin (6°45'N; 2°35' E). The rainfall in this area is bimodal with an annual mean of 1200 mm. The mean annual temperature varies between 25 and 29 °C and the relative humidity between 69 and 97%. Seeds were sown at an equal depth; one in each of 120 pots (5.5 cm × 18 cm) made from a polythene bag and filled with forest soil. The nursery period was 30 days. The pots were watered twice a day (morning and evening) throughout the duration of the experiment. The pots were arranged in a randomized complete block design with three replicates (or blocks). Each replicate was composed of 40 pots. The pots were kept in a weaning shed to reduce evaporation. At the end of this period, growth characteristics (stem height, collar diameter, biomass of leaves, number of leaves and root length) were measured.

Forty eight seedlings were planted in new plastic pots (36 cm × 32 cm) filled with forest soil. The pots were arranged in a randomized complete block design with

6 replicates (or blocks). Each replicate was composed of 8 pots. Every 30 days, one replicate was randomly selected for measure of growth characteristics. Each of the eight plants of the selected replicate was cut at the collar with a secator. The roots were extracted from the pot and the stem was isolated from the leaves with secator. The different organs were weighted with an electronic balance with precision of 0.0001g.

Sixty seedlings were used for a field experiment. The experimental units were arranged in a randomized complete block design with three replicates (or blocks). Each replicate was composed of 20 seedlings. The seedlings were planted at 1m × 1m spacing and an equal depth. The experimental units were watered twice a day (morning and evening) throughout the duration of the experiment. Stem height, collar diameter and number of leaves were measured on selected seedlings with replication each 30 days during 180 days (6 months).

Simulation model

The simulation model was based on the plant growth model published by Sønderskov *et al.*, 2006, which is a metabolic pool type model (Gutierrez, 1996; Gutierrez *et al.*, 1999). For details and mathematical description we refer to these publications and to Appendix 1, where the special elements used in this paper have been described. The input parameters have been given in Appendix 2.

When running a metabolic pool type simulation model, the first step is to calculate the amount of sugar being produced by photosynthesis, which is dependent on solar radiation, temperature, and the leaf area. The second step is to distribute the produced sugar to the different organs of the plant according to where it is demanded, and according to a row of priority. The row of priority in woody plants is fruits, flowers and buds (fruits, flowers and buds are not important when simulating young trees only) and then roots, leaves and aerial wooden parts (trunk and branches) according to their demands. All plant organs in the model have minimum required nitrogen

contents, and the photosynthesis efficiency of the leaves is dependent on the nitrogen contentment. Therefore, the uptake of nitrogen is important and is simulated as being dependent on the root biomass. Consequently, removing roots will reduce the nitrogen uptake efficiency and result in a nitrogen shortage. On the other hand removing leaves reduces the photosynthetic active leaf area and thereby affects the production of photosynthetic material resulting in a shortage of available carbohydrates for growth. In order to make the model capable of responding to utilization of leaves and roots, nitrogen deficiency changed the row of priority when distributing the photosynthetic material to give roots higher priority than trunk, branches and leaves. Similarly a shortage of photosynthetic material will cause the model to give priority to producing more leaves. This means that harvesting roots will cause the simulated tree to prioritize replenishing these roots, and harvesting leaves will cause it to give priority to replenishing the leaves. These priorities are in line with optimal partitioning theory (Bloom *et al.*, 1985; Gedroc *et al.*, 1996).

In this paper we describe different uses of the model. First, the model was calibrated to simulate the observed growth data from the nursery (calibration). Second, the model was used to simulate the growth of the plants from the field experiment (initial validation). Third, it was used to simulate how to optimize the utilization of leaves only, fourth, roots only, and fifth, both leaves and roots at the same time. The simulations were carried out using different density and nitrogen level.

The models were run for 3½ year only, because it was assumed to be the longest acceptable period based on the available growth data on *C. bonduc*. The model was parameterized by aid of nursery data from a period of about 9 months (Fig. 1) and validated against independent field data from the same period of time (Fig. 2). The lack of validation over the 3½ year period means that the results must be regarded hypotheses that should be confirmed by field data before being regarded as facts.

Results

Simulation of nursery and field experiments

The model was calibrated to simulate the development of the data from the nursery (Fig. 1) and was able to simulate the general trend, but was not able to simulate all data points precisely. The simulations of the biomass of stems, height and collar diameter coincided well with observations, but the data on biomass of leaves, number of leaves and roots were so irregular that the model was not able to capture the irregularity (Fig. 1). Especially the very irregular data points from the third and fourth sampling event were impossible to simulate precisely. With the simulation of field experiment (Fig. 2), the model was found to simulate the development in number of leaves and height very well as the simulations coincided very well with the observations.

Utilization of leaves or roots only

The optimal picking strategy depends on the time scale of the model. If the time scale is only 200 days after establishment, the optimal strategy was to pick a large fraction of the leaves as late as possible (Fig. 3A), but when increasing the time scale to 3½ years, the optimal strategy shifted to picking only between 10 and 20% of the leaves at a high frequency, such as about every 20 days (Fig. 3D). The yield was almost independent on when the utilization was initiated (Fig. 4), *i.e* the model suggests that farmers can start getting an income quickly without reducing the total yield over a 3½ year period. However, the yield was lower the last year if picking was initiated early.

The results concerning the utilization of roots were different from the results of the leaves as the optimal strategy under all timescales was to utilize (dig up) a fraction of the roots every 60 days, the longest possible interval. With the short time range of 200 days the optimal utilization level was 60% (Fig. 5A) and this shifted down to the lowest simulated utilization of only 10% (the lowest value simulated). Like for the leaves, the yield was almost independent on the time of initiating the utilization (not shown).

Utilization of leaves and roots at the same time

The simulations above were made using 1 plant m⁻² but in order to investigate the importance of plant density on the yield, the following simulations were made using densities of 1, 5 and 25 plants per m². The highest yields of both roots and leaves were obtained in the scenarios with 25 plants per m² (Fig. 6, 7 and 8) and high nitrogen levels (Fig. 8). At this plant density, the utilization intervals, every 40, 50 and 60 days, showed high yields for roots and best yields for leaves at the medium utilization frequencies of 10-20%. At

high plant density, the highest utilization frequency, every 10 days, utilizing only 5%, showed good yields for roots at low nitrogen levels, but rather low yields for leaves at the same utilization frequencies (Fig. 6E, F). High utilization levels showed generally low yields although there is a tendency to relatively high yields at high utilization levels at the highest nitrogen level (Fig. 6, 7 and 8). At high plant density and high nitrogen level the highest utilization frequency, every 10 days, showed high yields at large utilization levels for leaves, but low for roots (Fig. 8E, F).

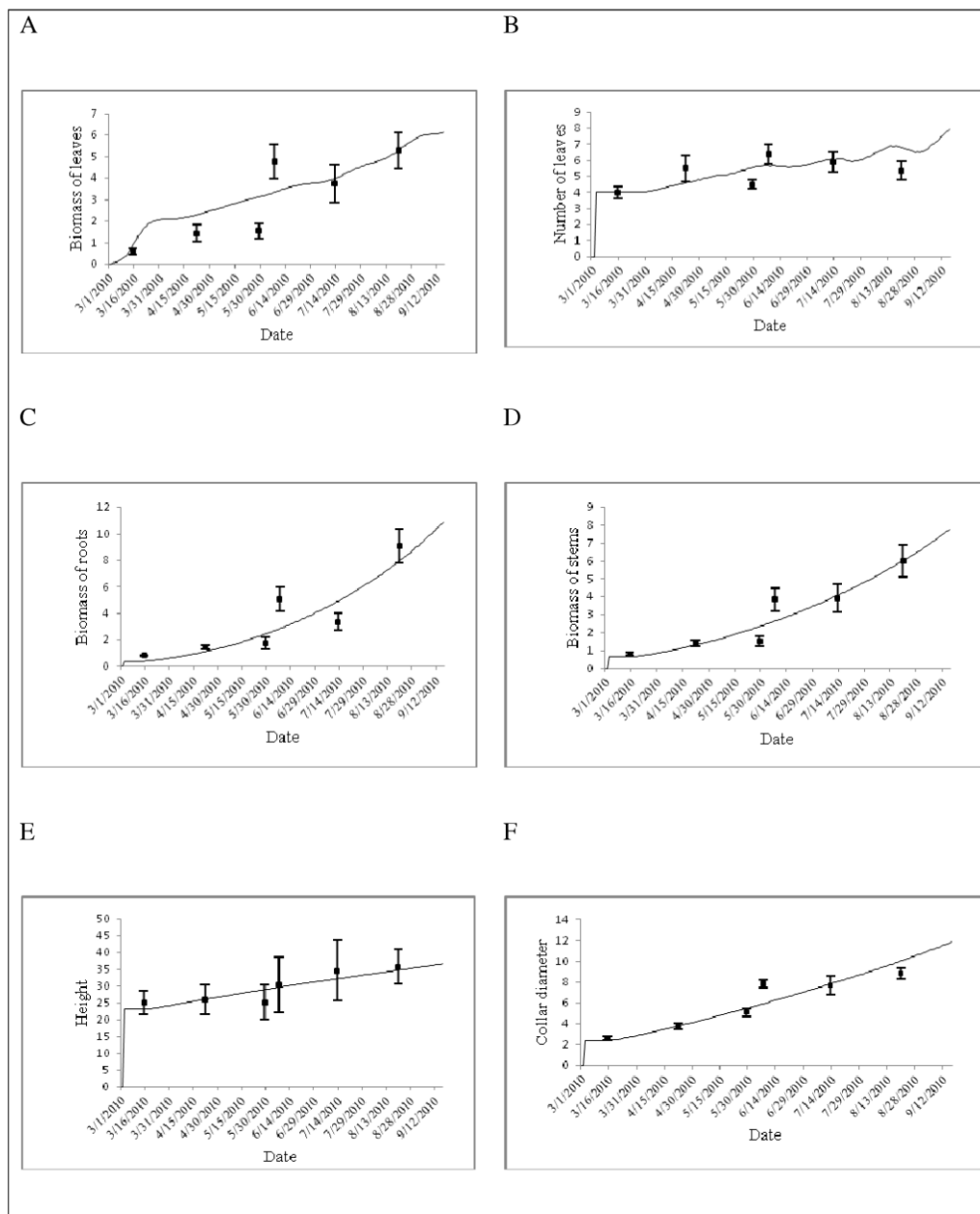


Fig. 1. Comparison between observations from nursery experiment and simulations of the development of biomass of leaves (A), number of leaves per tree (B), biomass of roots (C), biomass of stems (D), height in cm. (E), Padonou *et al.*

and collar diameter in cm. (F). Full lines show simulations and dots observations. Biomasses are in units of g per tree. The vertical lines are standard errors (SE).

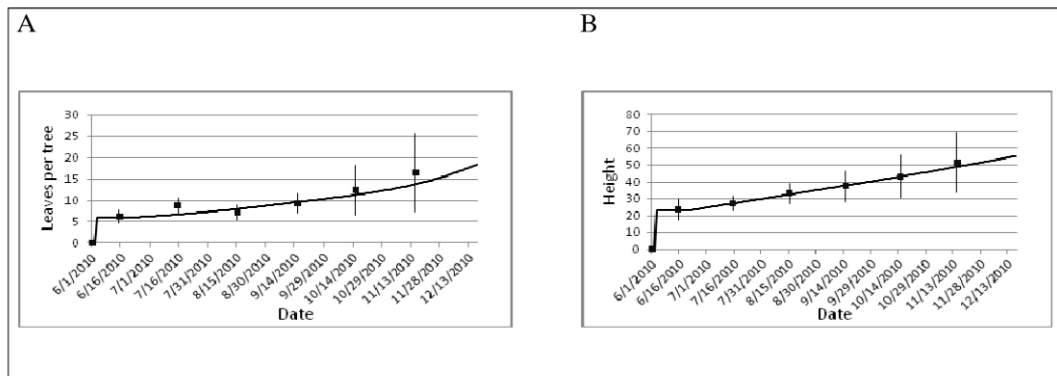


Fig. 2. Comparison between observations from field experiment and simulations of the development of number of leaves per tree (A), and height in cm. (B). Biomasses were not measured in the field experiment. Full lines show simulations and dots observations. The vertical lines are standard errors (SE).

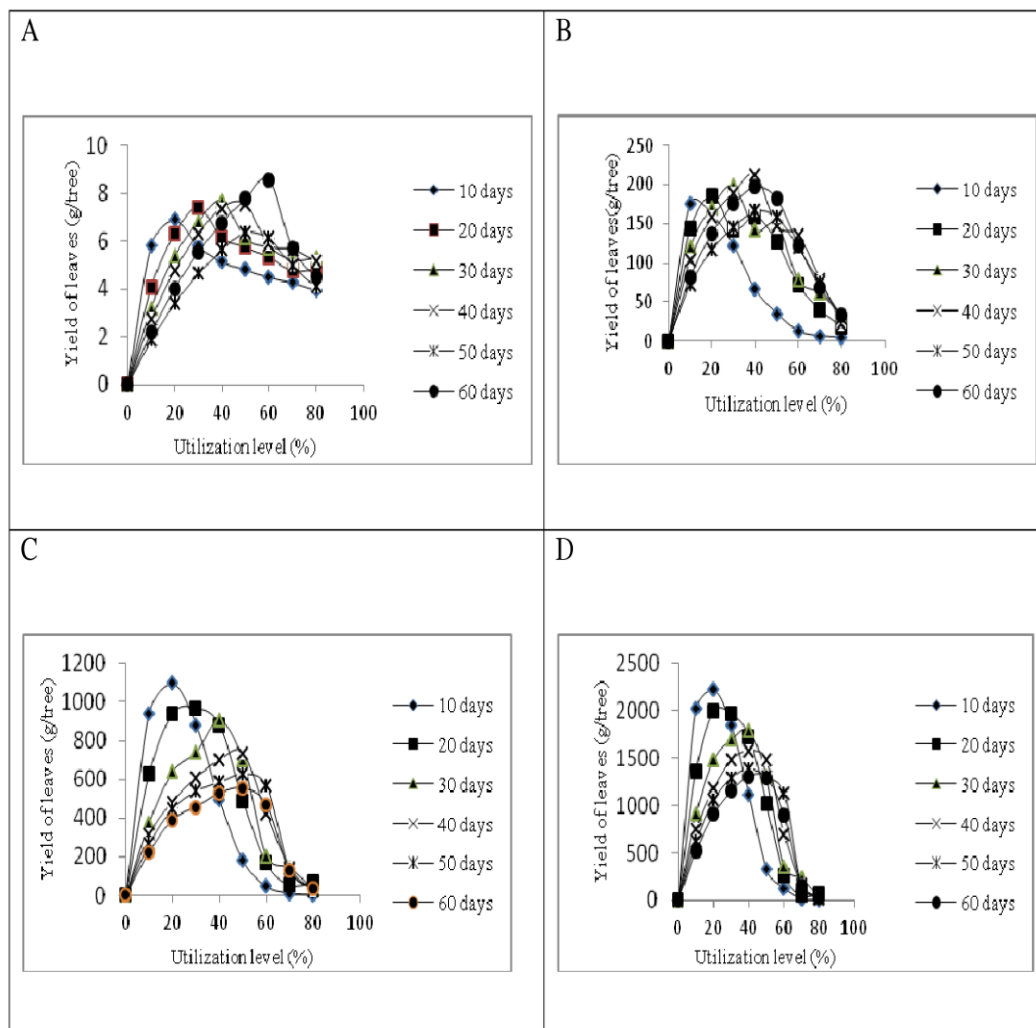


Fig. 3. The yield of leaves (dry weigh) vs. the utilization level for different utilization frequencies (every 10 days to every 60 days) and time frame of the model. A: 200 days from the 1 June, B: 565 days, C: 930 days, and D: 1295 days. Mind the different scales on the y-axes.

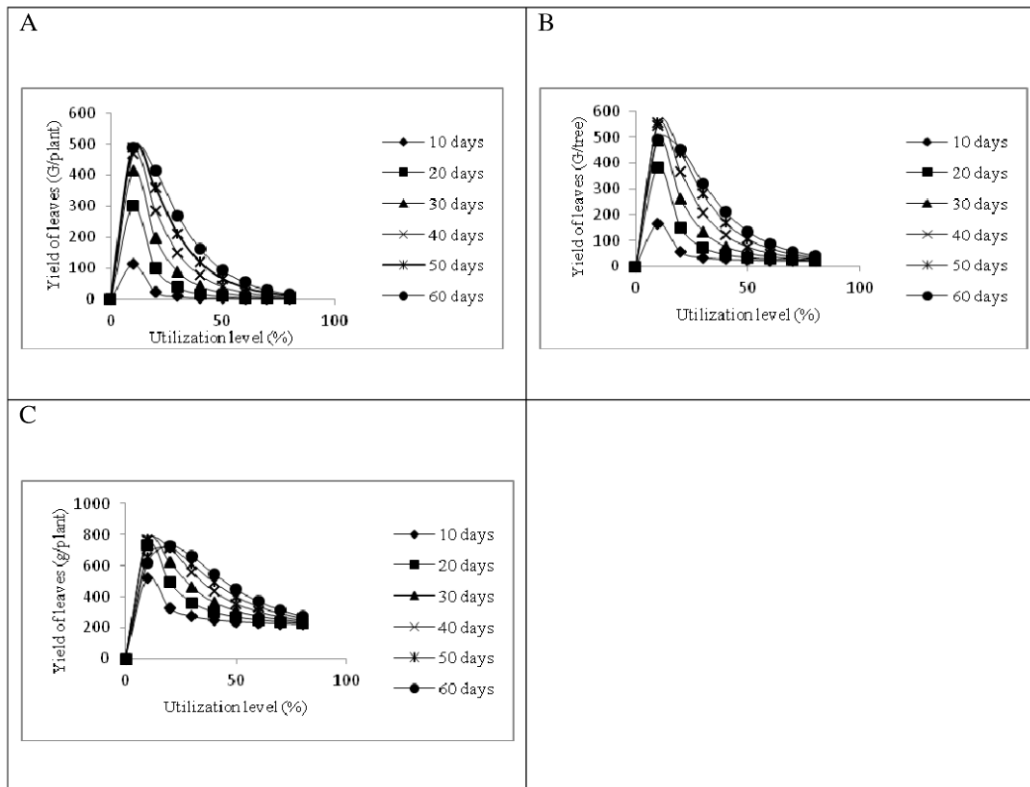


Fig. 4. The yield of leaves after 1295 days at different utilization strategies in relation to utilization frequency (every 10 – 60 days) and utilization level where the utilization was initiated after 2½ months (A), 1 year and 2½ months (B) and 2 years and 2½ months (C).

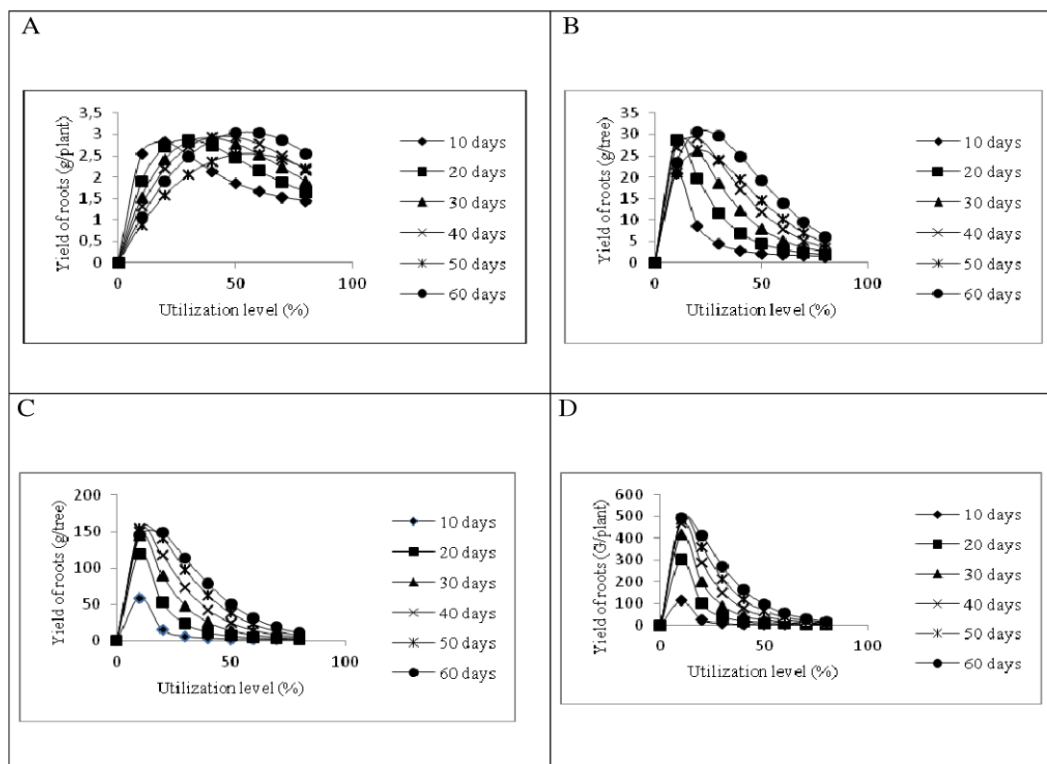


Fig. 5. The yield of roots vs. the utilization level depending on the utilization frequency (every 10 days to every 60 days). A: During 200 days from the 1 June (almost to the end of the year), B: During 565 days, C: during 930 days, and D: 1295 days. Mind the different scales on the y-axes.

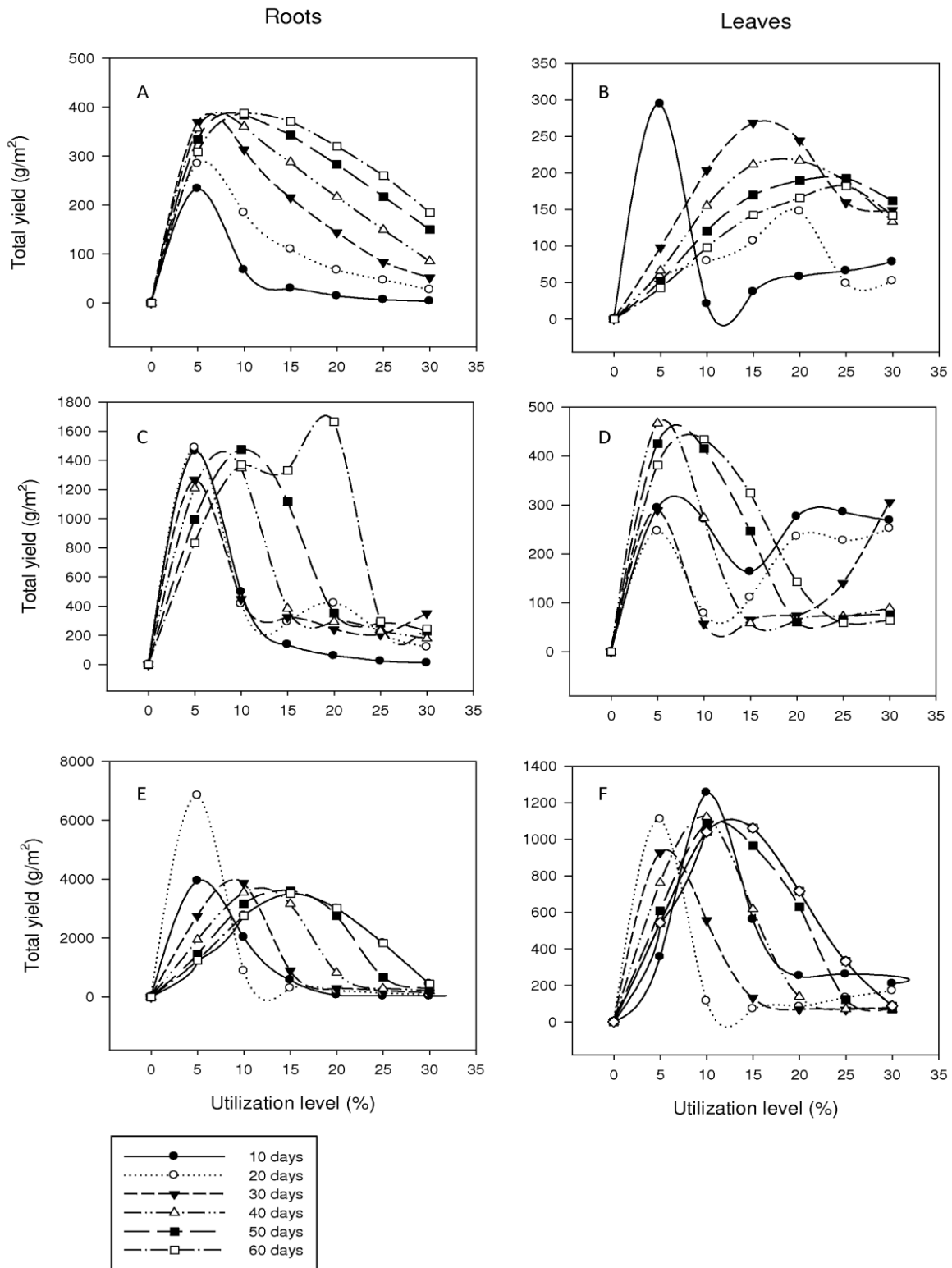


Fig. 6. The yield per m² of roots (left column) and leaves (right column) after 1295 days at a low nitrogen level at 1 plant per m² (upper row), 5 plants per m² (mid row) and 25 plants per m² (bottom row).

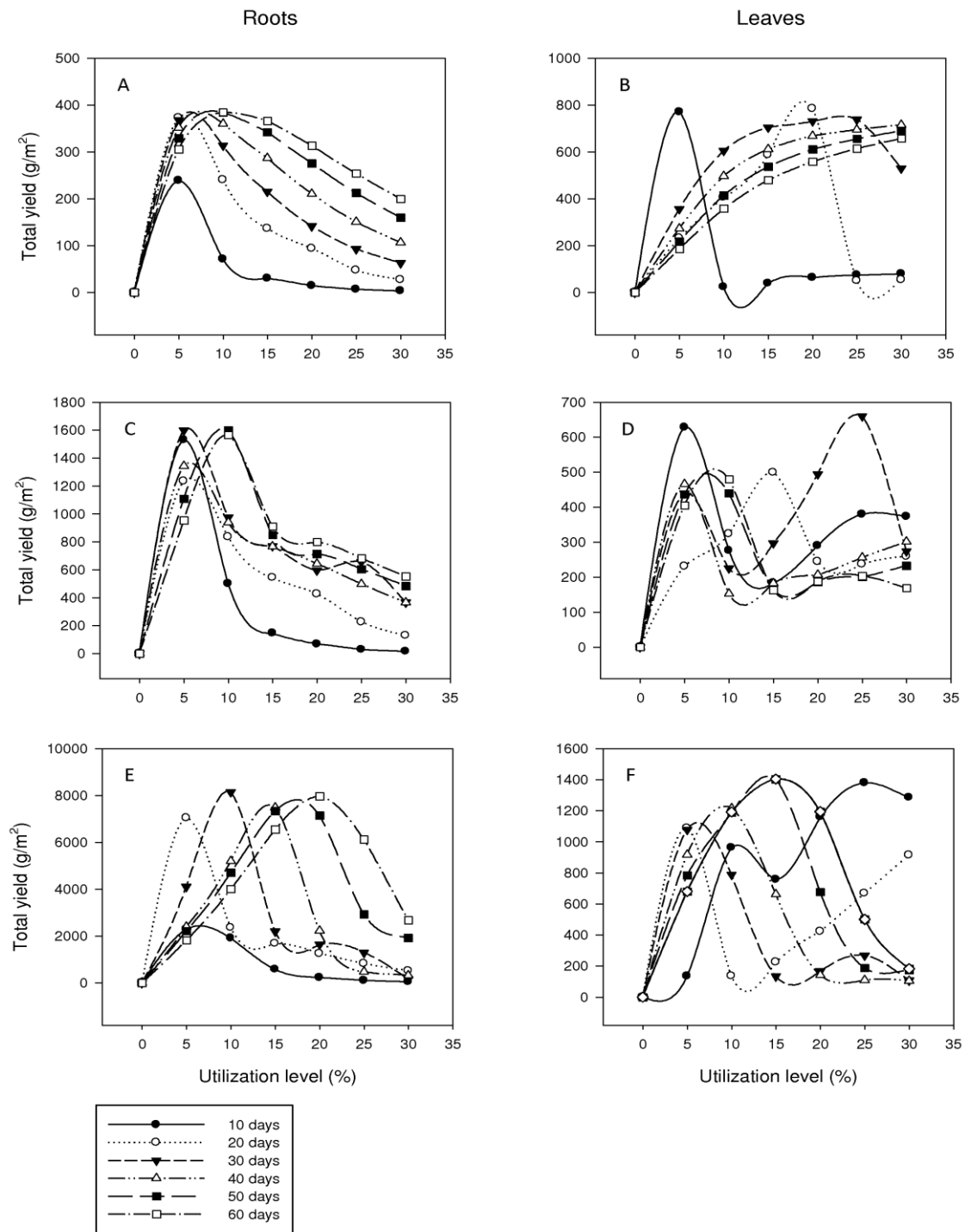


Fig. 7. The yield per m² of roots (left column) and leaves (right column) after 1295 days at a medium nitrogen level at 1 plant per m² (upper row), 5 plants per m² (mid row) and 25 plants per m² (bottom row).

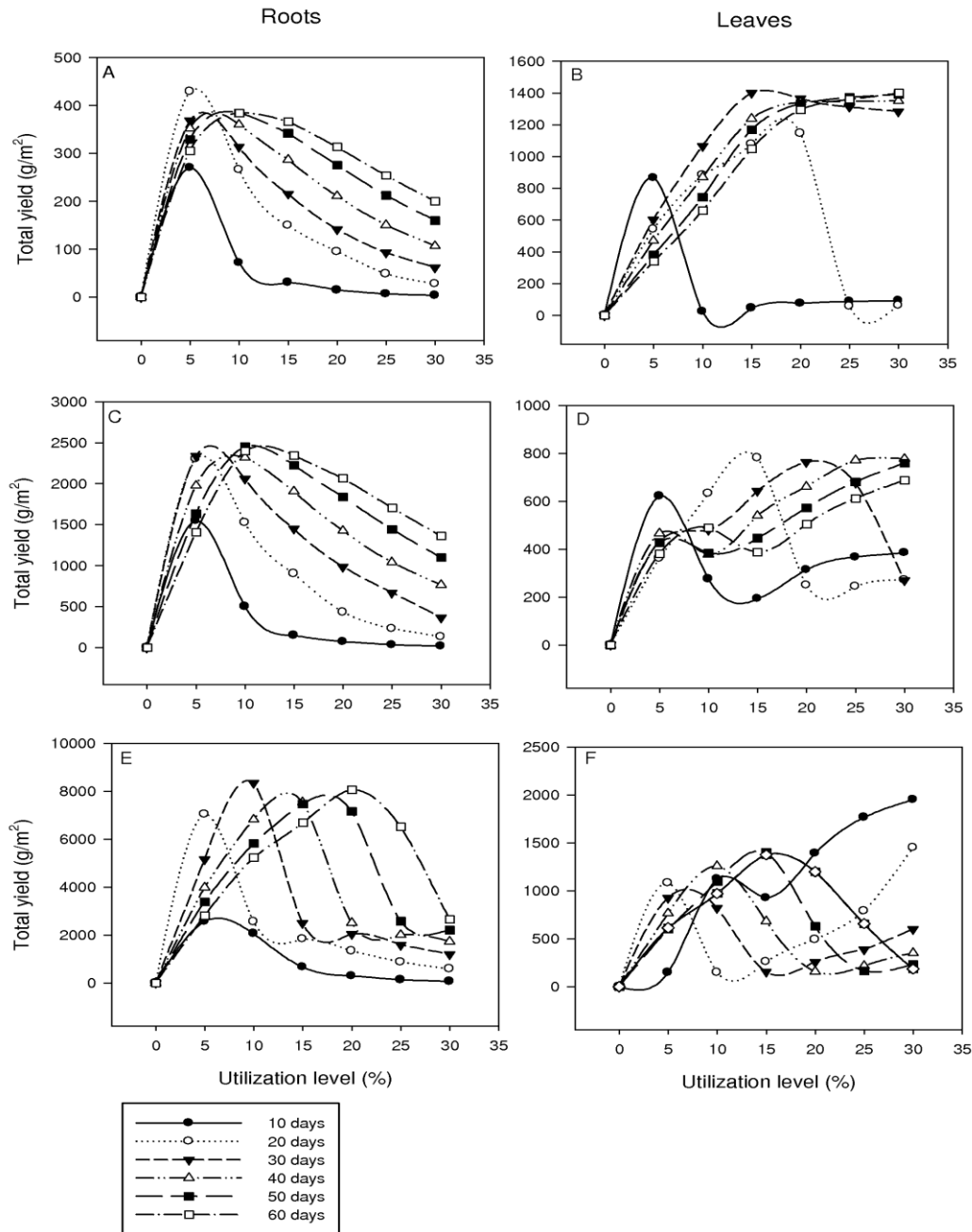


Fig. 8. The yield per m² of roots (left column) and leaves (right column) after 1295 days at a high nitrogen level at 1 plant per m² (upper row), 5 plants per m² (mid row) and 25 plants per m² (bottom row).

At low plant density (1 pr m²) the best yields of roots were obtained at low utilization levels and low utilization frequency (every 30 – 60 days), while the best yields of leaves were shown at medium utilization frequencies and medium utilization levels (Fig. 6A, B, Figure 7A, B, and Fig. 8A, B). At lower nitrogen levels, the combination of low utilization level and high utilization frequency (every 10 days) showed the best yield of leaves but lowest yield of

roots at the same combination (Fig. 6A, B, and Fig. 7A, B). In all combinations of plant densities and nitrogen levels, the yield of roots was simulated to be clearly higher than the yield of leaves (Fig. 6, 7 and 8).

Discussion

The simulations of the growth of *C. bonduc* in this study indicated that the productivity and dynamics of

the leaves and roots of the species are critical for the sustainable use of the species.

An efficient conservation and domestication programme of *C. bonduc* should be set up based on the present study and the existing results on its distribution (Assogbadjo *et al.*, 2012), germination and propagation (Hessou *et al.*, 2009; Tiwari *et al.*, 2010; Santosh Kumar *et al.*, 2012) and growth (under review). Such program will specify the rate of harvesting of the root and the leaves and prevent the overexploitation with negative impact on the sustainability of the species, especially in long term. Indeed, the species is characterized to date by a very low density and limited distribution of its populations in the wild. Participatory domestication of indigenous trees has been proposed as an appropriate means to alleviate poverty (Poulton and Poole, 2001), and could also have positive benefits on the environment since new plantings of *C. bonduc* would help to restore the declining resources of this important species.

The simulation models show that in order to optimize the utilization of *C. bonduc* it should be planted at high densities, grown at high nitrogen levels. Harvesting leaves and roots should take place every 50-60 days, and maximum 15% of the present biomass of roots and leaves should be harvested at each harvesting event. However, this conclusion depends on economic calculations which must be added to the simulation of yield presented here. Economic calculations must take the sales price of roots and leave, and the price of fertilizing the stand of tree into account, as well as the salaries to employees in case the owner is not the one doing the work of harvesting the roots and leaves.

Therefore, the results presented here are useful in the hands of growers or extension officers who have the necessary input to turn the results of our simulations into grower's revenues. In the present context where the species is threatened due to the overexploitation of its organs (mainly the roots), this conclusion is very important to design the appropriate condition for

plantation and harvesting period of leaves and roots for the different purpose. This is an important step for the sustainable use of the species.

The result that *C. bonduc* should be grown at high densities may be surprising but can be explained by the relatively short time horizon used in these simulations. Over a short period of time, it is important to reach an optimal utilization of the available resources of light and nutrients as quickly as possible, and this is done by planting high densities of trees. By planting, for instance, only one tree per 10 m² it will take several years to achieve a complete canopy cover to utilize the available solar radiation, but if 10 trees are planted per m² a complete canopy cover can be achieved rather quickly.

Our results suggest different utilization strategies depending on whether the grower wants to utilize roots or leaves. This suggests that growers may have to decide on focusing on either roots or leaves as it can be difficult to optimize both at the same time. However, our results also give indications on how to optimize yield of both roots and leaves at the same time. As the roots are more commercialized than the other parts (Vodouhê *et al.*, 2008) we may suggest the optimization of the use of the roots. However, this optimization may induce a death to the plant and limit its productivity. Considering the fact that the leaves and the roots are used sometimes for the same purposes (Assogbadjo *et al.*, 2011; Simin *et al.*, 2001; Kannur *et al.*, 2006; Datté *et al.*, 2004; Rastogi *et al.*, 1996), the optimization of the yield of both roots and leaves at the same time may be the appropriate strategy for the sustainable use of the plant organs.

The result that the total yield is not strongly dependent on the time when utilization is initiated is probably surprising, but it is important to keep in mind that an early utilization will cause a smaller harvest after 3 years, but the yield during the first 2 years compensates to some extent for this. However, a delayed start of utilization pays off in year 3 but growers may not be able to wait this long to get an

income, and the results here give some indications of the long term effects of starting the utilization early. The model presented here relies on many of the same principles as the modelling of coffee trees (Rodríguez *et al.*, 2011) and olive trees (Ponti *et al.*, 2013) by having: 1) detailed model units on the different organs of the tree, 2) being driven by the innate rate of increase, and 3) by being based on the physiological needs and climatic input. Unlike many other tree growth models that are using fixed distribution ratios between root and shoot (e.g. Simoni *et al.*, 2000), our model has a dynamic allocation between the different organs, that responds to the factor limiting the growth of the plant, i.e. the root growth gets high priority in case of nitrogen shortage, and leaves growth in case of carbon shortage. This means that the model tree will respond to root utilization that limits the nitrogen uptake by allocating resources to root growth which is in accordance with optimal partitioning theory (Bloom *et al.*, 1985; Gedroc *et al.*, 1996). This makes it very well suited to simulate the impact of utilization of roots and leaves on the continued growth.

It might be interpreted as a weakness of the model that it was not possible to calibrate it to simulate the growth in biomass of leaves and roots precisely (Fig. 1), but the data showed so large fluctuations between the third and fourth sampling dates that they must be ascribed to random sampling errors. Under relative stable weather conditions it is difficult to explain the fluctuations by other factors. Instead it supports the model that it is capable of well simulating the field data (Fig. 2), although it cannot be regarded a validation of the model. The model output has to be validated yet against field data covering a period of time similar to the period of the simulations presented in order to make the present results strongly trustworthy. Therefore the results can rather be regarded hypotheses, and used in designing the optimal field experiments.

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Appendix 1.

Here we give a summary of the plant growth model published by Sønderskov *et al.*, 2006 and a description of the modifications made to make the model capable of simulating the growth of tropical woody plants. The plant growth model published by Sønderskov *et al.*, 2006 is a metabolic pool type model (Gutierrez, 1996). For basic details and mathematical description we refer to these publications. The basic element of the model is a plant population (may consist of only one plant), and the growth of the population is simulated as the growth of coupled populations of plant organs (roots, leaves, stems, buds, flowers and fruits). The driving force of the growth of a population of plant organs is the innate demand for growth and reproduction and therefore each plant organ (except flowers and fruits) has a reproduction rate. This is the rate of production

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of new roots, new leaves, new stems and new buds, while there is no reproduction rate for flowers and fruits. Flowers are produced from buds that have finalized their development, and fruits are produced from flowers that have finished their bloom. Plant organs are in principle simulated as having a growing stage and a mature stage where the organ has reached the final size, which means that growing organs and mature organs are controlled separately in the model. However, buds and flowers are special in this respect because they only have one stage. Buds have no mature stage as mature buds burst into flowers, and flowers have no growing stage. In the model of Sønderskov *et al.* (2006) roots and stems had a growing stage and a mature stage, because the model was constructed to simulate annual weeds and grasses. In the present model it was necessary to reduce the number of stages of roots and stems

(trunks + branches) to only one, namely a developing stage, and this developing stage was given indefinite life time, because these two organs will persist during the entire life time of the tree, which was not defined in the model. In the model of Sønderskov *et al.* (2006) and the large number of models by Gutierrez and co-workers (e.g. Rodriguez *et al.*, 2011; Gutierrez *et al.*, 1999; Gutierrez, 1996), the population dynamics is controlled by distributed delays, which splits each stage into a number of sub-stages. A distributed delay can be regarded a kind of book keeping device, keeping track of the ageing and growth by aid of transferring matter from one sub-stage to the other, and while leaving the last sub-stage the matter is being transferred to the following stage, e.g. from growing stage to mature stage. As the life time of stems and roots is not defined in this model, the population dynamics of these organs was controlled by simple variables describing the numbers and biomass instead of using distributed delays (Severini *et al.*, 1998) that require a finite developmental time.

The model makes daily calculations of demand for photosynthates and nitrogen (split on demand for respiration, reproduction, growth and reserves) of each plant organ and this demand is the driving force of the simulation model. Following the calculation of the demand, the model calculates the supply of photosynthates and nitrogen for the plant growth based on the available light (available from climate files) and simulated amount of nitrogen in the soil. The distribution of photosynthates and nitrogen between plant organs depends on the priority between the organs and the row of priority within the organs (respiration, reproduction, growth and reserves). The priority between organs was made dependent on the nitrogen supply/demand ratio relative to the photosynthate supply/demand ratio. If the nitrogen supply/demand rate was lowest the roots were favored in the allocation of both nitrogen and carbon the following day making it possible for the plant/tree to acquire more nitrogen from the soil the following simulation days, and if the carbon supply/demand ratio was lowest this was interpreted

as a carbon shortage, and therefore the obvious reaction of the plant/tree was to increase the photosynthetic apparatus, e.g. leaves. This possibility of switching priorities between roots and aerial parts (all organs except roots) made it possible for the plant/tree to react to human utilization of either roots or aerial parts, i.e. after removal of either roots and/or leaves. Utilization of fruits, flowers or buds did not affect the allocation priorities. The calculation of the supply of photosynthates for the plant population was based on the photosynthesis of the leaves only and the uptake of nitrogen was based on the roots only, although the demands of the plant population was the sum of demands from all plant organs.

The demand for respiration was dependent on temperature and biomass of leaves, buds, flowers and fruits, but for the roots and stems the respiration was only made dependent on the mass of the actively metabolizing cambium layer between the wooden part of the trunk and the bark. For the rooting system this is supported by Pretzinger *et al.* (2002), who found a higher content of nitrogen in the finest roots of all investigated trees species from North America indicating a high metabolic activity in the finer roots, and by Makita *et al.* (2012), who found an increase in respiration with decreasing root diameter in 13 tropical tree species. Combining this with the fact that the finest roots also have the lowest “stele: root diameter ratio” (Guo *et al.*, 2008), and thereby the highest “cortex: root diameter ratio”, it seems to be reasonable to let the growth and respiration depend on an estimate of the biomass of the cambium layer and not on the biomass of the entire rooting system.

It has, however, not been possible to find literature on the biomass of the cambium layer in relation to the biomass of the shoot, and therefore an estimate of the cambium layer was assumed to be the same fraction of the bark layer, as the bark layer was of the total biomass of the stem/trunk. The simulation of the biomass of bark was done through calculations of the bark fraction of the total biomass of the stem/trunk, which varies with species and the size of the tree. Here an allometric relationship between diameter at

breast height DBH and the percentage of bark was used. Ter-Mkkaelin and Korzukhin (1997) have made a review of allometric relationships for the correlation between DBH and of different components of the trees for a long list of North American species, and their data on deciduous species were used to calculate average values of a and b for the allometric relationship (1). These average values were used in this model, because the species specific relationship was not known

$$B = a \times DBH^b / 100 \quad (1)$$

where B is the biomass fraction of bark, DBH is the diameter at breast height, and a = 0.02687 and b = 1.86913 are constants. Due to shortage of knowledge the same proportion of cambium layer was used for the roots as for the stems/trunks.

The vertical distribution of the plant organs was simulated by equation (2), which was modified from Graf et al. (1992)

$$p(x) = \left(1 - \frac{x}{h}\right) \times \left(\frac{x^{k_1}}{h^{k_2}}\right) \quad (2)$$

where p(x) is the biomass of a plant organ at the height x, h is the actual plant height, and k₁ and k₂ are constants. If k₁ = 4 and k₂ = 5 the equation will distributed the biomass as having the largest part close to the height h, and when using lower values of k₁ and k₂ such as k₁ = k₂ = 1 the distribution is almost even up through the vegetation layer. The assimilation of photosynthetic material follows the description of Graf *et al.*, 1990, Graf *et al.*, 1991, Gutierrez, 1996, but the canopy is split into a number of vertical zones, where the amount of solar radiation available for the second layer, is the global solar radiation minus what was assimilated in the uppermost layer. The solar radiation available for the third layer is the global solar radiation minus what was assimilated in the two uppermost layers, etc.

Appendix 2.

The parameters of *C. bonduc* in the simulation model and their origin. The allometric parameters were from the equation Mass = a×DBH^b where DBH is given in mm. and mass in g.

	Roots	Trunk	Growing leaves	Mature leaves
T0 (°C)	10 ^{a)}	10 ^{a)}	10 ^{a)}	10 ^{a)}
Developmental time/life time (D°)	No limit	No limit	250 ^{b)}	2500 ^{b)}
Initial mass (g)	0,0022 ^{b)}	0,0061 ^{b)}	0,0061 ^{b)}	
Creation rate (g/g /D°)	3.5×10 ^{-4 b)}	5×10 ^{-4 b)}	3.5×10 ^{-4 b)}	
Respiration rate (g/g /D°)	0.00883 ^{b)}	0.00883 ^{b)}	0.00883 ^{b)}	0.00883 ^{b)}
Growth rate (g/g /D°)	0.004 ^{b)}	0.020 ^{b)}	0.020 ^{b)}	
Allometric parameter a	0.131 ^{c)}	0.163 ^{c)}		0.11 ^{c)}
Allometric parameter b	1.764 ^{c)}	1.565 ^{c)}		1.767 ^{c)}
Max height (cm)		1000 ^{a)}		
Start height (cm)		23 ^{b)}		
Elongation factor		6×10 ^{-4 b)}		

a) Educated guess

b) Parameter fitted to simulate data from pot experiments

c) Parameter calculated based on data from pot experiments