Quassia amara L. diameter and total height under different light conditions: implications for the management of agroecosystems

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Abstract

Quassia amara L. is a semi-sciophyte species that can be found growing as a large shrub or a small tree in Neotropical rainforests. It is traditionally harvested as a non-wood forest product for culinary, medicinal and insecticidal uses. Lack of knowledge on the ecological conditions that support tree growth limits the development of sustainable forest management plans of natural forests and the development of new agroecological cultivation models.

The overall objectives of the present work are to i) compare the *Quassia amara* L. growth in different forest structures; ii) evaluate the impact of light conditions on *Quassia amara* L. diameter growth, total height growth and height–diameter relationship, and iii) discuss implications for the sustainable management of the species in agroecosystems. Light conditions are characterized at the tree level by the crown illumination index (cii), which is a visual and ordinal index.

Results show that tree growth varies between plots with different forest structures and light conditions. The cii was able to characterize light conditions. Best light conditions were different for diameter and total height growth: cii value of 5.0 (tree crown completely exposed to overhead and lateral direct light) and cii value of 3.5 (tree crown exposed to some vertical/overhead direct light and low direct light) respectively. The cii did not affect the height–diameter relationship. A value of cii equal to 4 was found as an intermediate condition and recommended for the establishment of new agroecosystems including the *Quassia amara* L.

Key words

Agroforestry; bitter wood; crown illumination index; mixed forests; non-wood forest product; light condition; *Simaroubaceae*; Costa Rica.

1. Introduction

The importance and variety of non-wood forest products (NWFP) is recognized around the world and for different reasons (e.g., FAO 1995; Wong et al. 2001; Shackleton et al. 2011; Shackleton and Pandey 2014), one being its contribution to increasing rural incomes associated with sustainable management practices taken in small-scale and family-owned farms, combining traditional knowledge with new societal demands and innovation (Ludvig et al. 2016; Pullanikkatil and Shackleton 2019). In Costa Rica and elsewhere in Central America, the number of trees, shrub and liana species traditionally used for their NWFP production is considerable (e.g., Nair and Latt 1998; Valle et al. 2000). It represents a large potential for local and regional development and poverty reduction (Pullanikkatil and Shackleton 2019), but it also requires some protection measures when they are present in the natural forest ecosystem (Wong et al. 2001).

Quassia amara L. (commonly known as hombre grande or bitter wood) is a species that can be found growing as a large shrub or a small tree in Neotropical rainforests (Croat 1978). According to Brown (1995) and Villalobos (1995), it is classified as a semi-sciophyte with high tolerance to shade conditions but with a requirement of direct exposure to sunlight in order to complete its life cycle, in particular due to its effect on flower and fruit production. An increase of the light conditions increases flower and fruit production although it does not influence seed fertility. Therefore, its natural regeneration appears to be limited by light and interspecific competition with upper-story forest species (Leigue 1997). Its distribution extends from Southern Mexico, through Central America, to northern South America, where it can be found in the Amazon Rainforest at altitudes ranging from sea level to 900 m (Brown 1995; Croat 1978). It is traditionally harvested in natural forests and used for culinary, medicinal and insecticidal purposes (Brown 1995; Ocampo 1995). Recently, it has also been increasingly studied and sought after for its efficacy in antiamoebic, antiplasmodial and antileukemic medicines (e.g., Bertani et al. 2006; Houel et al. 2009; Ocampo and Balick 2009), dermatologic and cosmetic uses (Burlando and Cornara 2017). This has resulted in increased interest in the species by rural communities (Ocampo and Rojas 2006) for the installation of new plantations in agroecosystems or for their extraction from natural forests.

The distribution, ecology and phenology of the *Quassia amara* L. have been studied in different regions from Costa Rica (e.g., Brown 1995; Villalobos, 1995; Cifuentes 1996; Leigue 1997). Although there are no studies or inventory data on the conservation status of the species' wild populations, Silva et al. (2001) refer to its endangered status in Brazil, and Ocampo and Rojas (2006) suggest the need for the development of sustainable agroecological cultivation models in Costa Rica in order to preserve the natural populations. This requires both knowledge of the relationship between environmental conditions and tree growth and the availability of models for the simulation of growth and production (Vanclay 1994; Burkhart and Tomé 2012). The present work contributes to fill this knowledge gap.

The objectives of the present research are i) to compare tree growth in different plots characterized by different forest structure types; ii) to understand the impact of light conditions on *Quassia amara* L.'s diameter growth, total height growth and height–diameter relationship, using the tree crown illumination index (cii) proposed by Clark and Clark (1992). iii) discuss implications for the sustainable management of the species in agroecosystems. The results allow us to discuss recommendations for the installation and sustainable management of new agroecosystems, such as agroforestry systems or mixed forests that include *Quassia amara* L., and the management of natural forests where the species is naturally distributed in Costa Rica.

2. Materials and Methods

2.1 Location and environmental description

The data sets were collected in the municipality of Talamanca, Limón province, Costa Rica. The region is naturally occupied by humid tropical forests, characterized by an annual mean temperature of 20ºC, 2300 mm of annual precipitation falling over an average 190 days per year, with no presence of a dry season (Solano 1992). There are on average 4.1 (July) to 5.9 (March and April) hours per day of direct solar radiation (measured by a heliograph), with an average value of 5.0 hours (Ministerio del Ambiente y Energía 2013). The soils in the region are predominantly Ultisols (IUSS Working Group WRB 2006).

2.2 Data collection

The first data set, referred to as the permanent plot data set from now on, was collected in eight permanent plots. One of the plots was installed in the natural forest of the Kekoldi indigenous reserve (9°38'N; 82°48'W). The remaining seven plots were installed in two private farm plantations (9°45'N; 82°55’W and 9°32'N; 82°37'W). The private farm plantations of *Quassia amara* were mainly installed in 1992. Only one of the plantations was planted in 1993 due to technical constrains in the previous year. The trees were planted after one year of growth in the nursery (two years after for the plot that was installed in 1993). The seeds used for the plantations were collected in the natural forest of the Kekoldi indigenous reserve. These eight plots differ in topographic location and forest structure type, representing a diverse range of growth conditions where *Quassia amara* L. can be cultivated or naturally found (Table 1). Three additional tree species occur in cultivation with *Quassia amara L.* in each one of the mixed stands:

- *Caryocar glabrum*, a native tree with a dense and spreading crown, which usually grows unbranched up to 25 m, traditionally harvested from natural forests for local use, a source of soap and wood. It is also cultivated for its fruit.
- *Magnolia mexicana*, a large native tree, growing up to 30 m, traditionally harvested from natural forests for food flavouring, medicine and as a source of wood.
- *Theobroma cacao*, a small native tree, growing up to 8 m with a globose crown, widely cultivated in lowland tropical areas around the world for its seed, which is a source of chocolate.

Table 1 here

According to the established forest inventory procedures defined by Marmillod et al. (1995), annual measurements of tree diameter at 0.3 m (d03) and tree total height (ht) were taken between the installation year 1995 and 2000. When a tree presented more than one shoot below 0.3 m height, individual shoots were measured separately. For each individual tree or shoot, the total number of branches at 1 m height (nbt) was recorded. Since 1997, light conditions for each tree were recorded annually using the ordinal crown illumination index (cii) proposed by Clark and Clark (1992). This index scores the source (vertical/overhead and lateral) and the relative amount of crown exposure to direct light:

1 – no direct light received by the crown either from overhead or side;

1.5 – low direct light received laterally, and no overhead light received;

2 – medium direct light received laterally, and no overhead light received;

2.5 – high direct light received laterally, and no overhead light received;

3 – some overhead direct light received (10% to 90% of the crown area exposed to vertical direct light), and no direct light received laterally;

4 – full overhead light (more than 90% of the crown area exposed to vertical direct light), and no or low direct light received laterally by the crown;

5 – crown completely exposed to overhead and lateral direct light.

The crown illumination index has been largely used for characterizing natural forests growing conditions in Neotropical rain forests (e.g., Cifuentes 1996; Clark and Clark 1999).

The second data set, referred to has the Kekoldi natural forest inventory data set (NatForest_KK_invent), was obtained during a forest inventory carried out in the natural forest of the Kekoldi indigenous reserve (Table 1). Trees are naturally regenerated, and their age is unknown. The management of the reserve by local communities includes the random cutting of some trees (Marmillod et al. 1995), but other than that the trees grow up to an unknown age. The forest inventory was carried out for the first time in 1997 and repeated in 1998, 1999 and 2000 (4 measurements). During this inventory, the same variables were measured at the tree level: d03, ht, cii and nbt. Summary statistics of both data sets are presented in Table 2.

Table 2 here

2.3 Data analysis and modelling

The first step was the graphical analysis of the permanent plot data set by plot and measurement, considering the d03 and ht measurements. The NatForest_KK_invent data set was not included in this step due to the lack of information regarding tree age and the unevenly aged structure of the natural forest. A t-test, performed for $\alpha = 5\%$, was carried out for the comparison of the d03 and ht mean values between plots using the TTEST procedure of SAS software (SAS Institute

Inc. 2011). The COCHRAN option was included in order to account for unequal variances between plots. This step allowed a first analysis of differences between plots that was later on followed by a modelling approach considering plot random effects.

The following step was an age-independent modelling approach carried out by the development of individual tree growth models for d03, ht, and a d03-ht relationship model. Growth models consist of equations that simulate the increment of each tree during a determined growth period (e.g., Burkhart and Tomé 2012). The measured growth is known to be the result of the interaction between the intrinsic tendency of the plant toward unlimited increase (biotic potential) and the restraints imposed by environmental resistance (growing conditions) and aging (e.g., Zeide 1993). Modelling the tree growth when age is not known is often necessary, for example, in old stands characterized by slow growing species, forest inventories, or in natural forests (e.g., Tomé et al. 2006). Although tree age was known for all except one of the plots of the permanent plot data set, it was not so for the Kelkoldi data set due to the fact it was collected in natural forests. Moreover, because of the limited range of ages available (1 to 8 years), the age variable was not considered an independent variable in the models. Instead, and according to the objectives of the work, testing the significance of the cii variable measured at the tree level in the model parameters allowed us to research the effect of different shading conditions on individual tree growth. The nbt value was also tested in the growth models and d03-ht relationship model parameters.

Due to the short interval between two consecutive measurements (annual interval) and limited range of tree ages available, linear growth models were considered suitable and fitted for the d03 and ht growth models. Each model is formulated as:

$y(t+1)_{ijm} = a + b\ y(t)_{ijm} + e_{ijm}$,

where y(t) is the tree diameter at 0.3m or the tree total height measured in year t, ‘a’ and ‘b’ are model parameters, i is the tree, j is the plot, m is the measurement, and e_{ijm} is the model error.

For the height-diameter relationship, a set of candidate models were considered. Paulo et al. (2011) suggest that the function form used to model the height-diameter relationship should be increased monotonically and have an upper asymptote. The candidate functions fulfil these requirements. They were the ones proposed by Paulo et al. (2011) based on the extended list proposed by Huang et al. (2000) but restricted to pass by (d03 ; ht)=(0 ; 0.3) point for the present data set (see Table 2 in Paulo et al. 2011).

Our analytical approach was similar for both models, although the first step was only carried out for the height-diameter model:

i) Selection of the best-fitting model by the ordinary least squares method, setting all model parameters as free. In this step, the selected function was the one resulting in the lower value of mean square error (MSE) and the highest value of adjusted r^2 (adj-r^2).

ii) Fitting of the model, including the plot random effect parameter, in all model parameters (e.g., Pinheiro and Bates 2000).

iii) Testing of the statistical significance ($\alpha = 5\%$) of cii and nbt variables in all model parameters. The variables were tested in three distinct forms, resulting in the fitting of a set of alternative models:

   a. Linear (the more the better): $a = a_0+a_1 X_{ijm}$
   b. Parabolic (an optimum condition exists): $a = a_0+a_1 X_{ijm} + a_2 (X_{ijm})^2$
   c. Hyperbolic (a maximum/optimum and asymptotic condition exists): $a = a_0+a_1 / X_{ijm}$, where ‘a’, ‘a_0’, ‘a_1’,

   where ‘a’, ‘a_0’, ‘a_1’, ‘a_2’ are model parameters, and X_{ijm} is d03 or ht from tree *i*, in *j* plot and *m* measurement.

iv) Comparison of the alternative models fitted in the previous step using the Akaike information criterion (AIC), and selection of the final model (lowest AIC value).

v) Evaluation of the model residuals variance by plotting the conditional studentized residuals as a function of the predicted value and of the model residuals normality by the normal probability plots of the conditional studentized residuals (e.g., Pinheiro and Bates 2000).

This approach allowed us to research the impact of light conditions at the tree level on *Quassia amara* and identify the plots where significant differences remained unaccounted for (when plot random effects appear significant in the final model). The fitting of the models was carried out using the nonlinear least squares method implemented in the MODEL and NLINMIX procedures of SAS software (SAS Institute Inc. 2011).

3. Results

3.1 Graphical analysis to the permanent plot data set

Plots in the permanent plot data set revealed significant differences in the d03 and ht of the trees, that increased with consecutive measurements (Figure 1). Differences were more pronounced for d03 than for ht.

Since the first measurement, carried out at 3 years of age, plot PP_Quassia+cacao_2 was outperformed by all other plots for both variables. The same behaviour was not observed by plot PP_Quassia+cacao_1, which was characterized by the same tree species composition. PP_Quassia+cacao_1 presented average values of d03 located in the central area of the figure and values of ht close to the plot with the largest measured values (PP_Quassia+Caryocar_1). A large dispersion of d03 and ht values was noticed in several plots, expressed by the large range values from the box plot upper and lower fences. This feature increased in the last measurements, particularly for d03 values of PP_Quassia+Caryocar_2 and PP_Quassia+cacao_1.

Identifying the plots with larger d03 and ht values across the measurements did not show clear evidence for one single plot. Plot PP_Quassia_pure_2 maintained larger d03 values over all measurements, but plot PP_Quassia+Caryocar_1 had higher mean ht values over time. Regarding d03, PP_Quassia+Caryocar_1, PP_Quassia+Caryocar_2, PP_Quassia_pure_1 and PP_Quassia+cacao_1 plots presented similar and intermediate values, with the first two reaching higher values that the last two after six years of age. For ht similarities between plots measurements were more evident for plots PP_Quassia+Caryocar_2 and PP_Quassia+Magnolia as well as PP_Quassia+cacao_1, PP_Quassia_pure_1 and PP_Quassia_pure_2.

Figure 1 here

The t-test (values not shown) confirmed the statistical significance of the some of the previous graphical observations regarding average values. The no rejection of the null hypothesis occurred when comparing the average values of plots PP_Quassia+Caryocar_2 and PP_Quassia+cacao_1 for mean d03 values, for ht values of plots PP_Quassia+Caryocar_2 and PP_Quassia+Magnolia, and for ht values of plots PP_Quassia+cacao_1 and PP_Quassia_pure_2.

3.2 Diameter growth model

Differences in tree d03 values and d03 growth between the plots were observed when plotting two consecutive measurements (Figure 2). NatForest_KK_invent data set showed the largest d03 values with a maximum of 11.5 cm. For the permanent plot data set, PP_Quassia_NatForest plot was the one presenting larger d03 values at the last measurement (maximum d03 value 8.6 cm), followed by PP_Quassia_pure_2 (maximum d03 value 7.5 cm). Tree d03 growth was observed in Figure 2 by the vertical distance of one observation to the bisector line. It showed that plot PP_Quassia_NatForest d03 is limited and overcome by other permanent plots in general. For the NatForest_KK_invent data set, d03 growth was variable.

Figure 2 here

The inclusion of the nbt variable in the model parameters resulted in non-significant estimates of the model parameters, showing that the variable does not influence d03 growth. The final fitted model included the cii variable in a parabolic form in the intercept parameter and two plot random effects in the intercept and slope parameters (Table 3).

$$d03_{t+1} = 0.1685\ \ cii - 0.0177\ \ cii^2 + u_0 + (1.0168 + u_1).\ \ d03_t$$

The significance of the plot random effect parameters in the intercept (‘u_0’) for plots PP_Quassia+Caryocar_1 (0.2030), PP_Quassia+cacao_1 (-0.1257), PP_Quassia_NatForest (-

0.1883), PP_Quassia_pure_2 (0.1779), PP_Quassia+cacao_2 (-0.1458) and the NatForest_KK_invent data set (-0.1988) showed that differences in d03 between plots remain unexplained by the model. The positive value of the random effect parameter showed a higher d03 estimated value in plots PP_Quassia+Caryocar_1 and PP_Quassia_pure_2, while the negative random effect associated to PP_Quassia+cacao_1, PP_Quassia_NatForest, PP_Quassia+cacao_2 plots and the NatForest_KK_invent data set shows that these are related to lower d03 growth. A significant random effect of the plot in the slope parameter ('u_1'), which is associated to a higher value of growth rate of d03, was only observed for plot PP_Quassia+cacao_1 (0.0411).

Table 3 here

In this model, the maximum value for the intercept parameter occurs when cii is 4.8, a value close to 5.0 that corresponds to the maximum cii value according to the Clark and Clark (1992), characterizing a tree crown that is completely exposed to overhead and lateral direct light. Considering the population effect (setting u_0 and u_1 parameters to zero (Paulo et al. 2011)) and an average tree size from the data set with a $d03_t$ of 3.5 cm, it's estimated value of $d03_{t+1}$ is higher if the light conditions are characterized by increasing cii values with a maximum obtained for a cii value close to 5.0. A tree of the same size, growing in the same plot but with lower access to light, will have a lower d03 growth (Figure 3).

Figure 3 here

The plot of the conditional studentized residuals showed that homoscedastic conditions were fulfilled and that normality conditions were considered acceptable (Figure 4).

Figure 4 here

3.3 Total height growth model

The inclusion of the nbt variable in the model parameters showed that the variable was not significant for the ht growth (parameter estimates not significantly different from zero). The final fitted model included the cii variable in a parabolic form in the slope parameters (Table 4).

$$ht_{\mathrm{t+1}} = 45.8725 + \mathrm{u}_0 + \left(0.8580 + 0.0527\ cii - 0.00751\ cii^2 + u_1\right)\ ht_{\mathrm{t}}$$

Table 4 here

The maximum value for the slope parameter (ht growth rate) occurs when cii is 3.5, a value that characterized tree crowns exposed to some vertical or overhead direct light and low direct light received laterally by the crown. Considering the population effect (setting u_0 and u_1 parameters to zero (Paulo et al. 2011)), one can estimate that an average tree with ht_t of 3.5 m will present a higher estimated value of ht_{t+1} if the light conditions are characterized by an intermediate cii value close to 3.5 (Figure 3).

The significance of the plot random effect parameters (Table 4) in the intercept was obtained for plots PP_Quassia+Caryocar_2 (20.8893), PP_Quassia_NatForest (-33.5354) and PP_Quassia+cacao_2 (-24.0540). Significant plot random effect parameters in the slope parameter (ht growth rate) were found for the same plots PP_Quassia+Caryocar_2 (-0.07579), PP_Quassia_NatForest (0.05426) and PP_Quassia+cacao_2 (0.06120).

The plot of the conditional studentized residuals showed that homoscedastic conditions were fulfilled and that normality conditions were considered acceptable (Figure 4).

3.4 Height-diameter model

The relationship between these two variables demonstrated the existence of an asymptotic value of ht when d03 values increase, which is distinct between the plots of the data sets (Figure 5).

Figure 5 here

The fitting of the models showed that for the ones including three parameters, convergence of the estimates was not obtained. Even if the fitting was carried out at the plot level, for the best definition of initialization values of the parameters, the differences between plots, expressed by distinct parameter estimate values (in particular between plots PP_Quassia+Caryocar_2 and PP_Quassia_pure_2 and the rest of the data set) did not allowed the convergence of these models. Among the other considered models characterized by two parameters, the selected one was:

$$ht = 0.3\ e^{\left[\frac{-a\ d03}{b\ (d03+b)}\right]}$$

When including the cii variable in the model parameters, similar AIC values were obtained compared to the previous model, demonstrating that cii does not influence the d03-ht relationship. When including the nbt variable in the model parameters, AIC values were reduced showing that the resulting models outperformed the previous one. The best results were obtained when the nbt variable was included in a hyperbolic form in parameter ‘a’ (Table 5):

$$ht = 0.3\ e^{\left[\frac{-(-3.6448+0.249/nbt+u_0)\ d03}{1.1423\ (d03+1.1423)+u_1}\right]}$$

This model showed that the ht asymptotic value will be influenced by the nbt value, varying between 9.10 m for one single shoot (nbt = 1) to 7.29 m when the nbt tends to large values.

The significance of the plot random effect was obtained when included in the ‘a’ parameter (‘u_0’) for the NatForest_KK_invent data set (0.1551), PP_Quassia+Caryocar_2 (0.2614) and PP_Quassia+cacao_2 (-0.3957) plots. In the ‘b’ parameter (‘u_1’) significant values were obtained for the NatForest_KK_invent data set (-0.1891) and PP_Quassia+Caryocar_2 (0.3786) plots. These random parameters showed that some differences remain unexplained regarding height-diameter relationship (Table 5).

The plot of the residuals showed that homoscedastic and normality conditions were fulfilled (Figure 4).

Table 5 here

4. Discussion

Quassia amara L. is described as a semi-sciophyte species with higher tolerance to shade but requiring direct exposure to sunlight during flowering and fruit production stages (e.g., Brown 1995; Villalobos 1995; Ocampo and Rojas 2006; Leigue 1997). This part of the tree's life cycle is essential for the establishment of natural regeneration, which can play a major role in large-scale landscape restoration in tropical regions (Chazdon and Guariguata 2016) and even surpasses active restoration practices in these natural forests (Crouzeilles et al. 2017). This feature is also encountered in other species producers of NWFP more extensively researched and found in tropical agroforestry landscapes such as *Coffea arabica*, *Camellia sinensis* L. and *Theobroma cacao* (Tscharntke et al. 2011). This evidences the importance of defining sustainable management plans for natural forests where NWFP are being extracted on the basis of reliable data collected with differentiated inventory methodologies and sampling schemes from forest inventories (e.g., Wong et al. 2001; Almeida and Tomé 2010). The inventories should not only allow the quantification of the species abundance and carbon stock but also of the natural regeneration, seed availability and characterization of light conditions. Proper inventory of NTFP stocks and research on NTFP ecology and sustainable harvest levels has been referred to as one of the eight crucial considerations for positioning NWFP on the development agenda by Shackleton and Pandey (2014), but these are still much less common than desirable around the globe and more so in tropical areas (e.g., Guariguata et al. 2010; Dhakal et al. 2016; Painkra et al. 2017). This work contributes to this cause with a focus on the *Quassia amara* L. species.

The differences in tree growth between the plots were clear in the two data sets. These differences were observed during the graphical analysis and by the significance of some of the plot random coefficients in the final models. These indicated that additional research on the effects of additional site variables affecting tree growth should be carried out. An important factor to consider is the tree species' arrangement and density, which was different in the permanent plot data set. In the PP_Quassia+Caryocar_1 and PP_Quassia+Caryocar_2 plots, for example, the

Quassia amara L. trees were planted in 3 x 3 m and in the middle of 4 *Caryocar glabrum* trees, while in the PP_Quassia+cacao_1 and PP_Quassia+cacao_2 plots the *Quassia amara* L. trees were planted intercalated with adult *Theobroma cacao* tree rows. The complexity of the subject, the range of possible combinations, the time associated with data collection of forest growth, and the increase of computation capacity has converged in the development of recent modelling approaches that can be considered (Rosskopf et al. 2017). Other factors that were not accounted for by the model were the topographic location and soil properties (depth, texture), which could influence water drainage, nutrient uptake and later on root development (Bellingham and Tanner 2006; Castilho et al. 2006).

Natural tropic forest areas are known for their high complexity in terms of light conditions, species composition, topography, etc. This leads to the development of variable environmental conditions that affect species distribution and growth in different ways. The data sets from natural forest areas (NatForest_KK_invent data set and PP_Quassia_NatForest plot) confirmed this high variability in terms of *Quassia amara* L. size. The fact that they included the highest values of d03 and ht was attributed to the presence of trees older than 7 years like the ones on the permanent data set, although age could not be determined. In terms of growth rates, the NatForest_KK_invent data set and the PP_Quassia_NatForest plot were associated to lower values, observed both graphically and by the negative values of the random coefficients of the fitted models. Excessive shading conditions and interspecific competition (e.g. Picard 2019) might be one of the causes of this slow growth that should be taken into consideration when defining management plans, in particular when considering d03 growth.

The two plots where the *Quassia amara* L. and *Theobroma cacao* species were mixed (PP_Quassia+cacao_1 and PP_Quassia+cacao_2) presented distinct results, but both were associated predominantly with negative values (when significant) of the plot random parameters of the fitted models. This was more evident for the d03 growth model. One plot was outperformed by the rest, while the other was able to reach average values of d03 and ht. The latter was installed in an area with a more variable topography (from a downhill to a hillside), and hypothesis about the influence of this variable in the variability of the measurements may be raised (Bellingham and Tanner 2006; Castilho et al. 2006). The *Quassia amara* L., when compared to the cacao tree, seems to have a distinct need for light during its life cycle. For cacao, shade is needed for young trees and is less important in older cacao plantations (Tscharntke et al. 2011). This suggested that the association of *Quassia amara* L. and *Theobroma cacao* species might not be favourable in mixed plantations, expect in areas were the last specie is characterized by older trees that might be pruned in order to increase light conditions to promote the *Quassia amara* L. growth and fruit production in case natural regeneration is one of the management purposes for the plantation. Although it was known that the *Theobroma cacao* trees was frequently pruned in the two plots, there were no records of dates when they occurred, their frequency, pruning intensity or the total height of these cacao trees. Since different tree height values and pruning practices may affect differently overhead and sided light conditions, this fact limited a more detailed analysis of the relationship between the two species.

The two plots where the *Quassia amara* L. and *Caryocar glabrum* species were mixed (PP_Quassia+Caryocar_1 and PP_Quassia+Caryocar_2) presented similar results regarding d03 growth as well as some of the larger values among all the permanent plots, appearing as a favourable species combination. Regarding ht growth, the plot behaviour was very distinct, and plot PP_Quassia+Caryocar_2 obtained similar results to the plot where the *Quassia amara* L. was mixed with *Magnolia mexicana* (PP_Quassia+Magnolia). With similar values of tree spacing and topographic conditions, it is not possible to clarify the reason for the differences in ht values for these plots. Information about the *Caryocar glabrum* and *Magnolia mexicana* trees crown (total height, base of the crown, etc.) and local soil characteristics could be variables related to these differentiated results.

The two plots installed in pure forest plantations (PP_Quassia_pure_1 and PP_Quassia_pure_2) had similar ht growth, but plot PP_Quassia_pure_2 outperformed for d03. Since the two plots are differentiated by their topographic conditions, with PP_Quassia_pure_1 being located downhill and PP_Quassia_pure_2 located on a hillside, one might again hypothesize, as for the *Quassia amara* L. and *Theobroma cacao* plots, that the downhill location had a negative influence on tree growth due to the reduction of water drainage in the soil.

Regarding the tree level differences, the data set included annual and individual tree level evaluation of the light conditions, which was characterized by the crown illumination index (cii) proposed by Clark and Clark (1992). The assessment of the cii provides a simple and rapid evaluation of light conditions, either by visual observation or hemispherical photographs analysis (Keeling and Phillips 2007), reducing time-consuming measurements of the surrounding tree height and crown dimensions. Results showed that this variable was related to both diameter and total height growth. This showed that cii could provide an effective characterization of growth conditions, even in a dynamic way if assessed through time, and therefore it could be used for inventory and management purposes. Since the cii is evaluated on the basis of the crown of the surrounding trees, irrespective of the species, it is particularly useful for natural forest areas, multi-species and multi-strata cropping systems like agroforestry systems.

The cii value contributing for larger d03 and ht growth was different for the two variables. After a stage of increasing ht for increasing cii light conditions, a maximum ht growth was obtained for cii equal to 3.5. Similar results were obtained for cii equal to 3 or 4. These values indicate that favourable conditions for the *Quassia amara* L. ht growth are characterized by partial to full overhead light and no or low direct light received laterally by the crown. The complete exposure of the crown to overhead and lateral direct light (cii equal to 5) induces a reduction in ht growth. Maximum cii values (cii equal to 5) maximize d03 growth. Even so, it was observed that the differences in d03 growth obtained under cii values of 4 and 5 are not large. Finally, cii values of 4 are found compatible, and intermediate conditions to both variables and were recommended as the best growth conditions for *Quassia amara* L. These suggested that the *Quassia amara* L. might be planted beneath and in the middle of taller tree species that provide lateral shade conditions (crown completely exposed to overhead and lateral direct light). These conditions might also be obtained by thinning and/or regular pruning operations of the taller tree species in the overstory, operations that can be an additional source of biomass, tree fodder and income for landowners (e.g., Salazar-Diaz and Tixier 2019). This issue leads to the open question related to the optimization of pruning intensity, frequency, crown pruning technics etc.

The present study contributed to existing literature on the determination of the relationship between light conditions and the *Quassia amara* tree species growth. It also contributed to the definition of suitable site characteristics and species combinations in agroforestry stands were *Quassia amara* may be included. Under sustainable management conditions, these are expected to help meet the increasing world demand of this species and avoid the overexploitation of the species in natural forests (Dawkins and Philip 1998; Sedjo and Botkin 2010; Silva et al. 2001). This work also raised awareness on the fact that the suitable conditions for *Quassia amara* L. wood production are still not fully understood. This is an essential step for increasing the awareness of farmers on the potential of the species. This knowledge gap contrasts with the growing knowledge of the chemical properties and industrial use potential of the species that ultimately presents a significant potential for increasing farmers' income and for the diversification of resources in forestry systems (e.g., Haggar et al. 1998), agroforestry systems (e.g., Salazar-Diaz and Tixier 2019) and/or agroecological production systems (e.g., Altieri 2002) in tropical areas.

5. Conclusions

Tree growth varies between plots with different forest structures and light conditions. Light condition, which is assessed at the tree level by the tree crown illumination index, was shown to be an important determinant of *Quassia amara*'s diameter and total height growth. Best light conditions are different for diameter and total height growth with intermediate values of cii (3.5) promoting total height growth and higher values (5.0) promoting tree diameter growth. Crown illumination index values of 4 are found compatible and intermediate conditions to both variables and were recommended as the best growth conditions for *Quassia amara* L.

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Figures caption

Figure 1. Box-plot of tree diameter at 0.3 m (d03) – top – and total height (ht) – bottom – measurements for the permanent plot data set. Data from Plot PP_Quassia_NatForest are not included since tree age is not known. The vertical bars on each box plot indicate the upper and lower fences, which are located at a distance of 1.5 times the interquartile range (IQR = Q3–Q1) above and below the box. Observations located outside the range of these bars are outliers and are identified by the isolated points.

Figure 2. Consecutive tree diameter at 0.3 m (d03) measurements (in cm), included in the permanent plots (top) and NatForest_KK_invent (bottom) data sets.

Figure 3. Tree diameter and total height estimates for year (t+1) obtained by considering distinct light conditions characterized by distinct cii values. The $d03_t$ and ht_t values were defined as the average values encountered in the data sets (d03 = 3.5 cm and ht = 350 cm). ht_t estimated values are presented in meters to facilitate the plot of the two series values.

Figure 4. Plot of the conditional studentized residuals as a function of the predicted value (left side graphics) and normal probability plots (right side graphics). Top graphics refer to the d03 growth model, middle graphics refer to the ht growth model (middle), and the bottom graphics refer to the d03-ht model.

Figure 5. Plot of total tree height (ht) against a diameter of 0.3 m (d03) pairs of measurements included in the permanent plots (top) and NatForest_KK_invent (bottom) data sets. d03 in cm and ht in m.

Table 1. Characterization of the permanent plot conditions: forest structure, topographic situation and number of trees.

Plot	Year of plantation	Site description	Stand structure	Topographic situation[1]	Plantation or forest area (m^2)	Plot area (m^2)	Number of trees in the plot
PP_Quassia+Caryocar_1	1992	*Quassia amara* plantation (3m x 3m), in a mixture with adult *Caryocar glabrum* trees. Each *Quassia amara* tree was planted in the middle of 4 *Caryocar glabrum* trees.	Mixed stand	Hillside	542	412	49
PP_Quassia+Caryocar_2	1992	*Quassia amara* plantation (3m x 3m), in a mixture with adult *Caryocar glabrum* trees. Each *Quassia amara* tree was planted in the middle of 4 *Caryocar glabrum* trees.	Mixed stand	Hillside	558	418	40

PP_Quassia+Magnolia	1993	*Quassia amara* plantation (3m x 3m) mixed with adult *Magnolia mexicana* trees. *Quassia amara* was in the middle of 4 *Magnolia mexicana* trees.	Mixed stand	Hillside	567	438	49
PP_Quassia_pure_1	1992	Pure forest plantation in rows (2.5m x 2.5m) in a previously natural forest area subject to clearing	Pure stand	Downhill	648	260	31
PP_Quassia+cacao_1	1992	*Quassia amara* plantation (3m x 3m) in rows, intercalated with adult *Theobroma cacao* tree rows. *Theobroma cacao was* frequently pruned.	Mixed stand	Downhill and Hillside	3460	760	52
PP_Quassia_NatForest	-	Natural forest. *Quassia amara* trees naturally regenerated.	Natural forest	Hillside	10000	1912	54

PP_Quassia_pure_2	1992	Pure *Quassia amara* plantation in rows (2.5m x 2.5m) in a previously natural forest area subject to clearing	Pure stand	Hillside	648	289.0	4677
PP_Quassia+cacao_2	1992	*Quassia amara* plantation (3m x 3m) in rows, intercalated with adult *Theobroma cacao* tree rows. *Theobroma cacao* was frequently pruned.	Mixed stand	Downhill	3264	760	49
NatForest_KK_invent	-	Natural forest. *Quassia amara* trees naturally regenerated.	Natural forest	Variable	-	-	402

[1] Downhill - Bottom of the slope, flat area; Hillside – high slope area, more than 40%; Tophill – transition between hillside and top of the mountain, with slope lower than 40%; Top of the mountain – flat and highly elevated area.

Table 2. Summary statistics of the measured variables included in the data sets.

Data set	Variable	minimum	mean	maximum	Standard deviation	mode
Permanent plots data set (n = 2222)	age	1	4.8	8	2.07	-
	d03	0.33	3.31	8.56	1.61	-
	ht	0.25	3.27	6.87	1.25	-
	cii	1.0	2.1	4.0	0.53	2.0
	nbt	1	1.50	9	1. 05	1
Kekoli data set (n = 2657)	d03	0.54	4.48	11.51	1.85	-
	ht	0.50	4.16	7.18	1.11	-
	cii	1.0	2.78	5.0	1.08	4.0
	nbt	1	1.26	6	0.68	1

Age – tree age (year). Information not available for plot PP_Quassia_NatForest. d03 – diameter at 0.3 m height (cm); ht – total height (m); cii – crown illumination index (Clark and Clark 1992); nbt – number of total branches at 1 m height.

Table 3. Parameter and covariance parameter estimates for the tree annual d03 growth model.

Parameter	Plot	Parameter estimate	Cov	Standard Error	Pr > |t|
a_1		0.1685		0.0202	<0.0001
a_2		-0.0177		0.0034	0.0001
b		1.0168		0.0101	<0.0001
u_0			0.0248		<0.0001
u_0	PP_Quassia+Caryocar_1	0.2030		0.0588	0.0006
u_0	PP_Quassia+Caryocar_2	0.0810		0.0506	0.1096
u_0	PP_Quassia+Magnolia	-0.0726		0.0469	0.1219
u_0	PP_Quassia+cacao_1	-0.1257		0.0498	0.0116
u_0	PP_Quassia+cacao_2	-0.1458		0.0408	0.0004
u_0	PP_Quassia_NatForest	-0.1882		0.0371	<.0001
u_0	PP_Quassia_pure_1	0.0951		0.0619	0.1243
u_0	PP_Quassia_pure_2	0.1779		0.0674	0.0084
u_0	NatForest_KK_invent	-0.1988		0.0294	<.0001
u_1			0.0007		<0.0001
u_1	PP_Quassia+Caryocar_1	-0.0055		0.0146	0.7070
u_1	PP_Quassia+Caryocar_2	0.0180		0.0137	0.1867
u_1	PP_Quassia+Magnolia	0.0100		0.0193	0.6041
u_1	PP_Quassia+cacao_1	0.0411		0.0140	0.0034

Table 3. Parameter and covariance parameter estimates for the tree annual d03 growth model.

Parameter	Plot	Parameter estimate	Cov	Standard Error	Pr > |t|
u_1	PP_Quassia+cacao_2	0.0076		0.0196	0.6968
u_1	PP_Quassia_NatForest	-0.0098		0.0125	0.4310
u_1	PP_Quassia_pure_1	-0.0347		0.0179	0.0521
u_1	PP_Quassia_pure_2	-0.0270		0.0148	0.0683
u_1	NatForest_KK_invent	0.0002		0.0103	0.9888
Residual variance		0.0375			

Cov - Covariance parameter estimates

Table 4. Parameter and covariance parameter estimates for the ht growth model.

Parameter	Plot	Parameter estimate	Cov	Standard Error	Pr > |t|
a_0		45.8725		7.4971	0.0001
b_1		0.8580		0.0243	<.0001
b_2		0.0527		0.0103	<.0001
b_2		-0.0075		0.0017	<.0001
u_0			383.67		<0.0001
u_0	PP_Quassia+Caryocar_1	18.5401		11.6183	0.1106
u_0	PP_Quassia+Caryocar_2	20.8893		9.6299	0.0301
u_0	PP_Quassia+Magnolia	-2.8077		9.5954	0.7698
u_0	PP_Quassia+cacao_1	-1.8218		10.9269	0.8676
u_0	PP_Quassia+cacao_2	-24.0540		8.9681	0.0074
u_0	PP_Quassia_NatForest	-33.5354		8.8013	0.0001
u_0	PP_Quassia_pure_1	7.6015		12.6068	0.5466
u_0	PP_Quassia_pure_2	16.1779		12.1179	0.1820
u_0	NatForest_KK_invent	-0.9900		7.9191	0.9005
u_1			0.0023		<0.0001
u_1	PP_Quassia+Caryocar_1	-0.0101		0.0275	0.7120
u_1	PP_Quassia+Caryocar_2	-0.0758		0.0297	0.0106
u_1	PP_Quassia+Magnolia	0.00525		0.0296	0.8593

Table 4. Parameter and covariance parameter estimates for the ht growth model.

Parameter	Plot	Parameter estimate	Cov	Standard Error	Pr > |t|
u_1	PP_Quassia+cacao_1	0.0305		0.0272	0.2614
u_1	PP_Quassia+cacao_2	0.0612		0.0299	0.0407
u_1	PP_Quassia_NatForest	0.0543		0.0243	0.0254
u_1	PP_Quassia_pure_1	-0.0191		0.0339	0.5743
u_1	PP_Quassia_pure_2	-0.0311		0.0307	0.3113
u_1	NatForest_KK_invent	-0.0152		0.0201	0.4511
Residual variance		1337.41			

Cov - Covariance parameter estimates

Table 5. Parameter and covariance parameter estimates for the tree height-diameter model (d03).

Parameter	Plot	Parameter estimate	Cov	Standard Error	Pr > |t|
a_1		-3.6448		0.2570	<0.0001
a_2		-0.2490		0.0226	0.0001
b		1.1423		0.0730	<0.0001
u_0			0.0427		<0.0001
u_0	PP_Quassia+Caryocar_1	-0.0529		0.0907	0.5595
u_0	PP_Quassia+Caryocar_2	0.2614		0.0987	0.0081
u_0	PP_Quassia+Magnolia	-0.1497		0.1251	0.2312
u_0	PP_Quassia+cacao_1	-0.0147		0.0886	0.8681
u_0	PP_Quassia+cacao_2	-0.3957		0.1406	0.0049
u_0	PP_Quassia_NatForest	0.0449		0.0870	0.6062
u_0	PP_Quassia_pure_1	0.0718		0.1064	0.4999
u_0	PP_Quassia_pure_2	0.0799		0.09670	0.4103
u_0	NatForest_KK_invent	0.1551		0.0787	0.0489
u_1			0.0467		<0.0001
u_1	PP_Quassia+Caryocar_1	-0.0213		0.1176	0.8560
u_1	PP_Quassia+Caryocar_2	0.3786		0.1347	0.0050
u_1	PP_Quassia+Magnolia	0.05474		0.1266	0.6655
u_1	PP_Quassia+cacao_1	-0.0873		0.1112	0.4324

Table 5. Parameter and covariance parameter estimates for the tree height-diameter model (d03).

Parameter	Plot	Parameter estimate	Cov	Standard Error	Pr > |t|
u_1	PP_Quassia+cacao_2	0.238		0.1293	0.0661
u_1	PP_Quassia_NatForest	0.0156		0.1002	0.8460
u_1	PP_Quassia_pure_1	-0.0922		0.1325	0.4865
u_1	PP_Quassia_pure_2	0.1575		0.1448	0.2768
u_1	NatForest_KK_invent	-0.1891		0.0787	0.0488
Residual variance		0.3497			

Cov - Covariance parameter estimates