

Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): Solutions to ambiguous field situations and description of the PCQM+ protocol

Farid Dahdouh-Guebas*, Nico Koedam

Biocomplexity Research Team c/o Laboratory of General Botany and Nature Management,
Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium

Received 3 December 2004; received in revised form 6 October 2005; accepted 24 October 2005

Abstract

This paper reports problems associated to the use of the Point-Centred Quarter Method (PCQM), as well as their possible solutions. Problematic settings in the application of the PCQM are amongst others due to the presence of multiple-stemmed trees (MST), to ambiguous settings for measuring the sampling point to nearest tree distance or the tree diameter, both of which may result in erroneous estimation of silvometric variables and parameters. The analysis is based on a database of effective individual tree records including distances, diameters, and heights measured in the field in a Sri Lankan mangrove forest between 1997 and 2002, and randomly compiles a series of records that were used as PCQM sampling points. Various structural forest parameters were calculated, with particular emphasis on density and basal area.

After proving that multiple- and single-stemmed trees have different silvometric characteristics, we adopted an empirical approach to demonstrate the classical PCQM protocol applied to MST generates significantly different densities (overestimation) and basal areas (underestimation) depending on which stems are considered for measurement, and we suggest an adapted PCQM+ protocol (measurement of central stem instead of nearest stem). We test both protocols in two mangrove assemblages (one composed of *Excoecaria agallocha* only, and an *Excoecaria agallocha*/*Rhizophora apiculata* mixed forest) with MST proportions varying between 0% and 100%, at 5% intervals.

The results indicated that the classical PCQM protocol generates density and basal area results that are strongly correlated with the MST proportion in the assemblage ($p < 0.001$), whereas the PCQM+ protocol shows a robustness with no such correlations for density. For basal area the results of the PCQM+ protocol showed a weak correlation with the MST proportion, and regression-ANCOVA results indicated that they were significantly different from those of the highly sensitive PCQM protocol ($p < 0.001$).

Finally, we conclude by writing out the entire PCQM+ protocol, elaborating on the solutions to other common problems related to ambiguous settings for the consideration of stems or the measurement of their diameter (aerial roots, split trunks, dwarf growth, horizontally developing stems, boundary of an individual in MST, selectively cut trees or tree parts, very sparse assemblages, use of PCQM for remote sensing ground-truth), and by nevertheless highlighting the potential of the PCQM/PCQM+ approach. Although we used a mangrove forest data set, the PCQ-Method and our suggestions are widely applicable to other forest types. In addition, this paper is accompanied by the first interface that automatically processes standard PCQM-related data (regardless of forest type) to generate common silvometric or forestry parameters elaborated in this paper, and it is freely available in Appendix C and from <http://www.vub.ac.be/APNA/staff/FDG/pub/pub.html>.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Forest; Mangrove; PCQM; Single-stemmed; Multi-stemmed; Density; Basal area; Silvometrics; *Excoecaria*; *Rhizophora*

1. Introduction

The study of forest structure or the management of a forest for silvicultural purposes requires that structural parameters

such as density, basal area and biomass are estimated. Although a number of studies report about the possibility to remotely sense such factors using aerial or landscape photographs (e.g., Brandtberg and Walter, 1998; Montès et al., 2000), or by using satellite imagery at finer scales (Holmgren et al., 1997; Holmgren and Thuresson, 1998), most studies involve the measurement of vegetation characteristics in the field for an assemblage or at the individual tree level. In order to do so a number of plot-based and plot-less phytosociological and

* Corresponding author. Tel.: +32 2 629 34 22; fax: +32 2 629 34 13.

E-mail addresses: fdahdouh@vub.ac.be (F. Dahdouh-Guebas), nikoedam@vub.ac.be (N. Koedam).

vegetational relevé methods exist (cf. Kent and Coker, 1992; Elzinga et al., 2001). Plot-based methods start from a plot with a known surface in which vegetation is characterised, whereas plot-less methods measure distances, and are based on a random distribution of trees. The Point-Centred Quarter Method (PCQM) of Cottam and Curtis (1956) is one of the plot-less methods that has been considered very efficient in characterizing vegetation, while minimizing damage to the forest understorey (Cunningham, 2001). It yields quantitative data by studying trees nearest to sampling points as an estimate of numbers and distribution (a more specific methodological protocol is given in the methodology section). Based on the measurement of different variables in each quadrant (quarter) of each sampling point, various forest structure parameters can be calculated. The PCQM is a method suggested to be appropriate for the investigation of forest structure in mangroves (Cintrón and Schaeffer Novelli, 1984), the forest ecosystem from which we used a data set in the present paper. It must however be highlighted that the method, our improvements to the method suggested in this paper, or the first application that we provide for data processing, are not dependent on forest type and can be widely applied beyond mangrove forests. Motivation to use of the PCQM rather than other plot-less methods or rather than plot-based relevé methods not only includes the statistically sound quantitative basis, but also logistic factors such as ease and speed with which the fieldwork can be executed in the tide-

subjected mangrove ecosystems. Although tree aggregation, as well as size-concentric tree organisation, a very frequent phenomenon in mangroves, has been recognised as a possible problem to the PCQ-Method (Cottam and Curtis, 1956; Cintrón and Schaeffer Novelli, 1984), the method has been widely applied. Until present no effort was attempted to our knowledge to evaluate this or other PCQM-associated limitations in any forest type.

As a result of mangrove fieldwork experience on basis of the PCQ-Method amongst others, we have realised that the use of the PCQ-Method is shrouded in more problems than commonly, if at all, highlighted. Dense root systems entangle propagules (Fig. 1), which may establish and create a situation in which the closest stem to a reference point is very often a younger and thinner tree or a secondary stem of a tree, and not the main stem of the individual or of the specimen at that location. Multiple-stemmed tree species such as *Excoecaria agallocha* L. give rise to similar field situations, as it comprises a number of thick central stems surrounded by many thinner stems (Fig. 1). The same may occur in multiple-stemmed *Avicennia* or *Rhizophora* species (Clough et al., 1997; Imbert and Ménard, 1997). Repeated consideration of the closer thinner stems only, may give rise to erroneous forest structure data, which is certainly undesirable in silvicultural practices – although knowledge of the entire community is required, silviculturists are interested in thick or regular exploitable stems for economic purposes (e.g., Kairo, 2001). In addition,



Fig. 1. (A) Scenery of an *Excoecaria agallocha* dominated mangrove forest in Galle. The complex of islets and pools is the result of burrowing activities by *Thalassina anomala*. (B) Close-up of a typical multiple-stemmed *E. agallocha* individual with thicker central stems surrounded by thinner stems. (C) Development of mangrove saplings (around a thicker tree), entangled by the root complex. (Photographs by Farid Dahdouh-Guebas and Griet Neukermans).

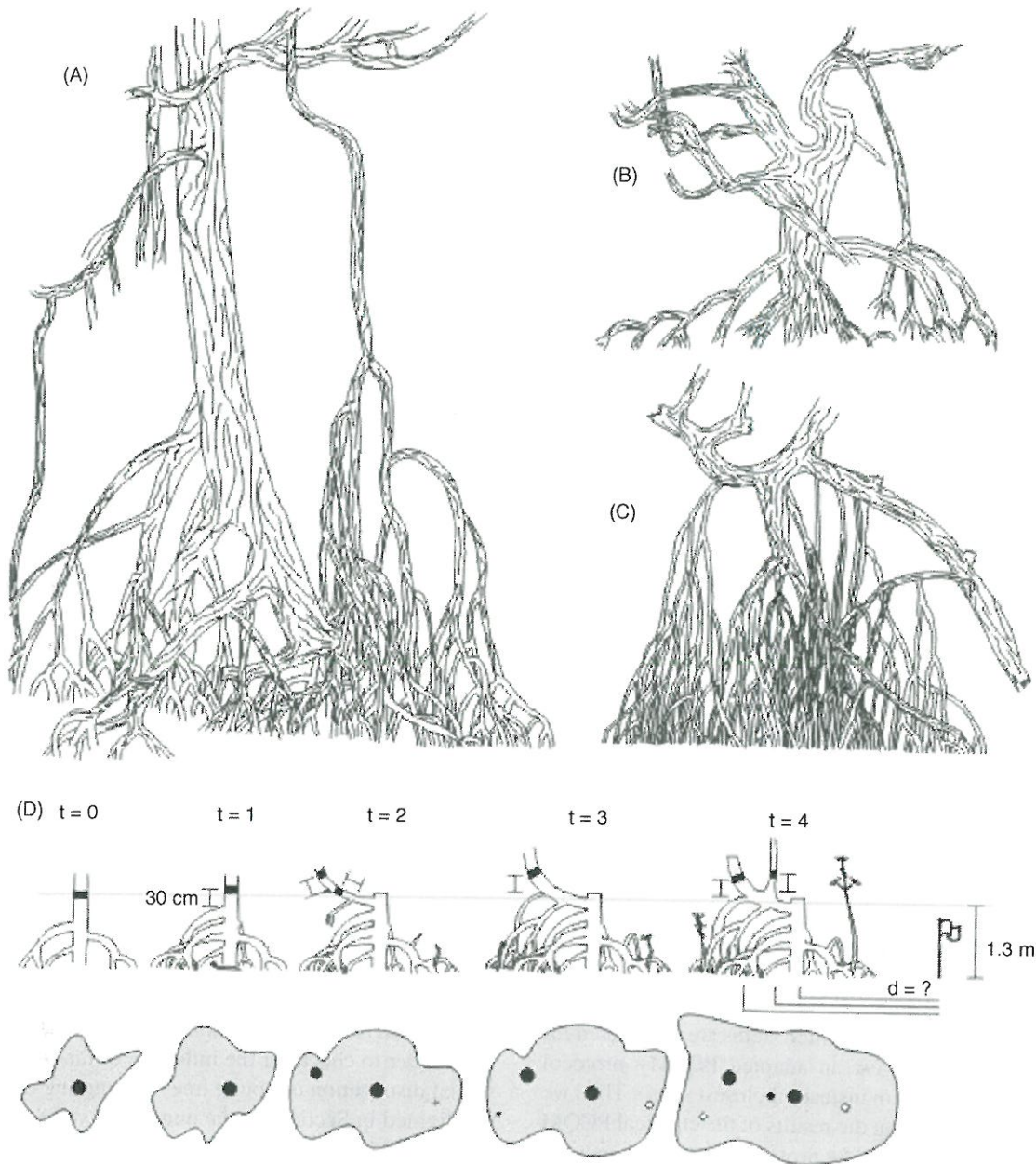


Fig. 2. (A–C) Three examples of *Rhizophora* trees drawn by hand in the mangrove to highlight the architectural complexity of this genus (up to which place should the sampling point to nearest tree distance be measured? Where exactly should the stem diameter be measured?). (D) Schematic of a *Rhizophora* mangrove (side view at the top and aerial view of root extent and stem position below) showing an unequivocal situation for measuring the tree diameter at 130 cm above the floor D_{130} ($t = 0$), and a further evolution scenario to highlight the complexity and ambiguities in the use of the Point Centred Quarter Method: a standardisation of +30 cm along the stem for the measurement of the D_{130} ($t = 1$ – 4), measurement of the diameter with respect to cut stems ($t = 2$ – 4) and with respect to developing roots ($t = 2$), and the measurement of the distance d from the (flagged) sampling point ($t = 4$). The figure also shows that in a future moment in time, the closest tree to a sampling point will not be one of the central *Rhizophora* stems, but one of the entangled propagules that are developing into young trees (possibly belonging to another genus). Black lines in bold indicate the theoretical possibilities of diameter measurement; ' $t = 0$ ' represents a certain moment in time and ' $t > 0$ ' for later moments in time.

multiple stems, cut stems or peculiar root and stem settings, may lead to ambiguities for actual measurement of representative diameters (Fig. 2). The latter is very frequent in *Rhizophora* species, which are species with a complex architecture naturally, but which accommodate selective cutting resulting in altered individual appearance as well as vegetation assemblage stand structure (Kovacs, 1999; Dahdouh-Guebas et al., 2000a,b; Kairo et al., 2002b; Dahdouh-Guebas et al., 2004a,b). The common existence of unusual

individual trees or tree clusters necessitates that a number of questions be answered:

- Which stem is representative in a multi-stemmed tree?
- How can relevé methods based on nearest individual (or nearest neighbour) distances account for artefacts caused by complex root systems?
- Considering that the PCQM requires recognition of individuals, what is the boundary between one individual

and another in multiple-stemmed trees? If this is ambiguous, is recognition of individuals essential?

- How must individuals and stems that are interconnected over a large root complex be approached?
- Does the approach change if such root connections break and individual stems continue to grow separately?
- Where should the stem diameter be measured with respect to prop roots? (Fig. 2A).

Simple measurement according to the classical PCQM protocol in any of the above situations may lead to an over-estimation of tree density and an underestimation of the basal area calculated on basis of the tree diameter. In addition, it may also lead to an erroneous species importance value, since adult trees with entangled roots and developing propagules that have been trapped by the root complex are not necessarily of the same species. This situation occurs for example in *Rhizophora* species, with younger individuals of the same or other species surrounding large *Rhizophora* trees (Kairo, 2001; Kairo et al., 2002b). The entanglement of propagules is also corroborated by the changing species composition over time in monospecific *Rhizophora* plantations (Bosire et al., 2003). Finally, considering that allometric relationships for estimating mangrove biomass are often based on the measurement of tree diameter (Suzuki and Tagawa, 1983; Woodroffe, 1985; Putz and Chan, 1986; Amarasinghe and Balasubramaniam, 1992a,b; Gong and Ong, 1995; Fromard et al., 1998; Saenger, 2002), it is obvious that there is also the risk of generating erroneous biomass results (cf. Brokaw and Thompson, 2000).

In this paper, first we prove that multiple- and single-stemmed trees have different forest characteristics. Second, we show that applying the Point-Centred Quarter Method to multiple-stemmed trees generates significantly different densities (potential over-estimation) and basal areas (potential under-estimation) depending on which stems are considered for measurement, and we suggest an adapted PCQM+ protocol (measurement of central stem instead of closest stem). Then we test the method by comparing the results of the classical PCQM protocol with that of the PCQM+ protocol in two forests (one composed of *E. agallocha* only, and an *Excoecaria agallocha*/*Rhizophora apiculata* mixed forest) in which the proportions of multiple-stemmed trees vary between 0% and 100%. Third, we conclude by writing out the entire PCQM+ protocol, elaborating the solutions to other common problems (aerial roots, split trunks, dwarf growth, horizontally developing stems, boundary of an individual in MST, selectively cut trees or tree parts, very sparse assemblages, use of PCQM for remote sensing ground-truth), and by nevertheless highlighting the potential of using the PCQM method.

Our objective is not to solve each of the questions addressed earlier in Section 1 by way of an empirical approach, but rather to report and help to solve the main problems associated to the use of the PCQM, the reliability of which is otherwise taken for granted. Our paper does, however, use an empirical approach for the two core silvometric attributes only (density and basal area), and intends to help dealing coherently with other reported problems, which are not investigated but usually solved ad hoc by surveyors.

2. Material and methods

2.1. Description of the study site

The methodology used in this paper is applicable to any forest type, but during our research we applied it to a mangrove forest. Located between Galle and Unawatuna (06°01'N–80°14'E) along the south-western side of the island of Sri Lanka in the wet climate zone (Mueller-Dombois, 1968), this basin and riverine mangrove forest type (*sensu* Lugo and Snedaker, 1974) covers an area of 1.5 km² and is located at about 600 m from the Indian Ocean shore. Two rivers run through the mangrove forest, namely the Thalpe Ela, discharging into the ocean, and the Galu Ganga, a tributary of the former. The species complex of the mangrove in Galle comprises *Bruguiera gymnorhiza* (L.) Lam., *B. sexangula* (Lour.) Poir., *E. agallocha*, *Heritiera littoralis* Dryand. and *R. apiculata* Bl. (all mangrove nomenclature according to Tomlinson, 1986). A few occurrences of *Lumnitzera racemosa* Willd., *Bruguiera cylindrica* (L.) Bl. and *Ceriops tagal* (Perr.) C.B. Robinson within the forest, and the presence of *Sonneratia caseolaris* (L.) Engler at the forest margins have been reported as well (Dahdouh-Guebas et al., 2000b; Jayatissa et al., 2002). The mangrove forest in Galle has been subjected to anthropogenic influence over the last 50 years and displays what has been labelled as a 'moving-mosaic' vegetation dynamic (Dahdouh-Guebas et al., 2000b; Dahdouh-Guebas and Koedam, 2002). In the mangrove forest of Galle there is no slope with upper or lower intertidal areas, but rather a mixture of islets and pools (Fig. 1), created by the mangrove mud lobster *Thalassina anomala* Herbst.

2.2. Methodology

2.2.1. Influence of root complex on propagule entangling

In order to check for the influence of the root system on the spatial distribution of young trees (entangling of propagules as highlighted in Section 1), the number of young stems standing amongst *Rhizophora* roots and those standing away from these roots were counted in a 1,000 m² sampling area dominated by *E. agallocha* and *R. apiculata*, with occasional occurrences of *B. gymnorhiza* (L.) Lam. To identify a 'young tree', the median diameter (5.09 cm) of all trees in the study site was rounded to the nearest 0.5 cm (in this case 5.0 cm), and this number was taken to be the maximum diameter for a 'young tree'. Young trees therefore measured between 2.5 cm (the minimum diameter recorded in the database) and 5.0 cm. We also used this value because in the field trees were always measured to the nearest 0.5 cm. This differentiation between young and adult trees also corresponds to common silvicultural interests and regulations in mangroves (e.g., Kairo et al., 2002a), and to our best professional judgement. However, we do highlight that different study aims may result in other definitions of adult, young or juvenile mangrove plants. For instance, Dahdouh-Guebas and Koedam (2002) defined these classes as stages in survival from impacts such as predation or physiological stress, with juvenile trees (= propagules with

maximum three leaf pairs) being prone to propagule predation, young developing trees (= trees smaller than 130 cm or with a tree diameter at 130 cm above the soil smaller than 2.5 cm) being prone to environmental stress, and adult trees being well established.

2.2.2. Differences between single- and multiple-stemmed *E. agallocha* trees

E. agallocha is without any doubt the mangrove species that is most often found as multiple-stemmed trees (far more often than for instance the well known *Rhizophora* species), and it is also the dominant species in our study site. From our database of vegetation and silvometric variables and parameters from 5 fieldwork expeditions to Galle between 1997 and 2002 (>1000 entries), we extracted the records of 860 different *E. agallocha* trees, with a majority of them listing measurements of sampling point to nearest individual distance (d), stem girth at 130 cm above the floor (G_{130}) and height (h). With ‘above the floor’ we also intend ‘along the stem’ (because not all stems are standing upright), but this will not be repeated throughout the text. The basal area (Ba) for a certain individual j was calculated from the stem diameter D_{130} (term according to Brokaw and Thompson (2000), but formerly referred to as DBH, the diameter at breast height) as follows (assuming that stems have circular cross-sections):

$$D_{130j} \text{ (in cm)} = \frac{G_{130}}{\pi}, \quad (\text{tree diameter}) \quad (1)$$

and,

$$Ba_j \text{ (in m}^2\text{)} = \frac{\pi \times (D_{130j}/2)^2}{10000}, \quad (\text{basal area}) \quad (2)$$

In the field, these data were originally collected along nine transects by sampling at 10 m intervals with the Point Centred Quarter Method. Each sampling point was divided into four quadrants (or quarters) as the PCQM prescribes. The orientation of the quadrants was at right angles of the transect direction. For each of the quadrants the nearest tree higher than 1.3 m and with a G_{130} larger than 8.0 cm (and thus a D_{130} larger than 2.5 cm), was identified with the rule of thumb that no tree was considered more than once. The distance of the sampling point to the centre of the tree was measured using a tape measure (5 mm accuracy) or a hand-held laser distometer (Disto Lite 4, Leica Geosystems AG, 5 mm accuracy), taking into consideration two important points. First, when using a laser distometer the laser dot is pointed to the outer

bark of the tree and is not measuring to the centre of the tree stem. Therefore, the distance d is computed by adding the radius of the tree to the distance read from the laser distometer. Second, for multiple stemmed trees we measured distance d with respect to the centre of the formation (i.e. to the visually estimated point of gravity of the multiple stems) and not to the nearest stem. Likewise, the diameter G_{130} was measured for the one or more central thicker stems of the formation, and their values were averaged during later parameter calculations. The consideration of the central stems, roughly located 0.5 m to 1 m farther than the marginal stems in *E. agallocha*, and between 1 m and 3 m farther in *Rhizophora* species, is new, and does not follow earlier descriptions by Cottam and Curtis (1956) or Cintrón and Schaeffer Novelli (1984). We will refer to the original description as the ‘PCQM protocol’ and to this new one as the ‘PCQM+ protocol’. Where it was not possible to measure the D_{130} for *R. apiculata* individuals (commonly because of the species’ root formation at 130 cm above the floor), the diameter was standard-wise measured 30 cm above the upper prop root originating from the central stem.

For all species present within the sampling area, between 24 and 272 trees per species were selected in the forest and for each tree the G_{130} and the height (using a Suunto hypsometer) was recorded in order to check whether a relationship between these two variables exists. The coefficient of determination (r^2) was tested (t -test) and was found to be highly significant ($p < 0.001$) for all the species (*B. gymnorrhiza*, *E. agallocha* and *R. apiculata*) and a regression was done to generate an equation for each species (Table 1). These equations were then used to extrapolate a height for each tree in the sampling area based on its D_{130} .

In the records extracted from our database, we separated the single stemmed trees ($n = 674$), hereafter referred to as ‘SST’, from the multiple-stemmed trees ($n = 186$), hereafter referred to as ‘MST’, and compared the means for each of the above factors by way of a t -test (two-sampling assuming unequal variances).

2.2.3. Dependence of silvometric parameter calculations on stem position within multiple-stemmed trees

In this part of the study we start by considering two mangrove forest assemblages, one assemblage purely consisting of *E. agallocha*, and an *E. agallocha*-*R. apiculata* mixed assemblage with 3:1 proportions for the two species, respectively. The proportions of the mixed assemblage are actually as observed for the majority of the areas within the forest of Galle (Dahdouh-Guebas et al., 2000b). We used the

Table 1
Coefficients of determination, t -test statistics and regression equations for the relationships between height h and tree diameter D_{130} in the mangrove species *Bruguiera gymnorrhiza*, *Excoecaria agallocha* and *Rhizophora apiculata*

Species	r^2	n	t	p	Regression equation
<i>B. gymnorrhiza</i>	0.45	24	4.24	<0.001	$h = 0.3195 (D_{130}) + 2.6314$
<i>E. agallocha</i>	0.45	272	14.94	<0.001	$h = 1.9455 \ln (D_{130}) + 1.0843$
<i>R. apiculata</i>	0.40	79	7.18	<0.001	$h = 1.7504 \ln (D_{130}) + 2.7038$

same database as described above to extract all data on *E. agallocha* and on *R. apiculata*. Based on these real data, we then extracted 80 different records, which would correspond to a PCQM method with 20 sampling points (with each containing 4 quadrants with tree data). Then the following parameters were calculated: the stem density (De) and basal area (Ba) for each species and for the entire mangrove stand, the mean stand height (\bar{h}), the complexity index (C.I.) of Holdridge et al. (1971), the relative density (De_r), the relative dominance (Do_r), the relative frequency (F_r), and the importance value (I.V.) of Curtis (1959) for each species. Apart from the calculation of mean stand height, which is straightforward, the formulas for the above parameters are given below (we refer to Cintrón and Schaeffer Novelli, 1984 who exemplify the calculation of these parameters):

$$De = \sum_{i=1}^m \frac{1}{(\sum_{j=1}^{n_i} (d_{ij}/n_i))^2}, \quad (\text{density}) \quad (3)$$

$$Ba = \sum_{i=1}^m \sum_{j=1}^{n_i} \frac{Ba_{ij}}{n_i}, \quad (\text{basal area}) \quad (4)$$

$$C.I. = \frac{m \times Ba \times \bar{h} \times De}{1000}, \quad \text{after Holdridge et al. (1971)} \\ (\text{complexity index}) \quad (5)$$

$$De_r = \frac{100n_i}{\sum_{i=1}^m n_i}, \quad (\text{relative density}) \quad (6)$$

$$Do_{ri} = \frac{100 Ba_i}{Ba}, \quad (\text{relative dominance}) \quad (7)$$

$$F_{ri} = \frac{100F_i}{\sum_{i=1}^m F_i}, \quad (\text{relative frequency}) \quad (8)$$

$$I.V. = De_{ri} + Do_{ri} + F_{ri}, \quad \text{after Curtis (1959)} \\ (\text{importance value}) \quad (9)$$

where d_{ij} is the sampling point to nearest tree distance for tree j of species i ; n_i , number of trees sampled for species i ; m , number of species; Ba_{ij} , basal area of tree j of species i (see also Eq. (2)); Ba_i , basal area of all trees of species i (see also Eq. (4)); \bar{h} , mean stand height; F_i , number of sampling points in which species i is represented times 100.

During our fieldwork expeditions we always measured the central stems of MST. In a first calculation representing the PCQM+ protocol, we selected records from adult trees only ($D_{130} > \text{median } D_{130}$ in entire database). In a second calculation representing the classical PCQM protocol, we substituted the d and the D_{130} for each record (sampled using the PCQM+ protocol) in such a way that it represents a tree standing closer and being thinner (just like an MST in a real situation, see Fig. 1). This substitution was done according to a number of sound rules. For the replacement of the D_{130} by that

of thinner trees we used the median of the D_{130} frequency distribution for all the representatives in our database (per species) to identify the limit between a thick and a thin stem (see also Section 2.2.1 and Fig. 3). For the replacement of d we subtracted a realistic distance between 0.5 m and 1 m for *E. agallocha* trees and between 1 m and 3 m for *R. apiculata* trees from the distance given in the selected record (see also Section 2.2.2 and Fig. 3).

In this calculation we thus confronted a PCQM simulation (or rather ‘compilation’) that always considers a closer thinner stem of an MST, with a PCQM+ protocol that always considers the central thicker stem of the MST. We compared the results between the PCQM and the PCQM+ protocol for a series of assemblage types in which the MST proportion varied between 0% and 100%, at 5% intervals, and each with 10 replicate compilations. Although a forest made out of MST only is rare in nature, the instructive value of this extreme range must be considered. The above was done for both the *E. agallocha* assemblage and the *E. agallocha*/*R. apiculata* mixed assemblage, amounting to a total of 860 simulations (2 assemblages \times 21 MST-proportions \times 2 protocols \times 10 replicates). We emphasize that the term ‘simulation’ is used to refer to the random selection of records from the database. The data in the database were not de novo computer-generated, but are real field data.

2.2.4. Observations on ambiguous settings for measurement

During 11 fieldwork expeditions of our team to Kenya, Sri Lanka and Mauritania (1997–2005) observations on peculiar and ambiguous tree settings were made in order to synthesize common problems with the PCQM and suggest solutions.

2.2.5. Statistical analysis

We calculated descriptive statistics for all the structural forest characteristics. We focused on density and basal area, and confronted the change in these parameters with the MST proportion for each of the protocols by calculating correlation coefficients of determination (r^2). Where the difference between the PCQM and the PCQM+ protocol was not clear, we performed a linear regression for each of the data sets and confronted the regression by way of analysis of covariance (ANCOVA).

3. Results

3.1. Influence of root complex on propagule entangling

The comparison of the spatial distribution of young trees in presence and in absence of *Rhizophora* roots clearly confirmed in practice the theoretical possibility that the root complex of *Rhizophora* entangles propagules as suggested in Section 1. In an area with roots there were 1557.6 young trees per hectare (this corresponds to 6.42 m² available surface per tree), which is significantly larger (by a factor 20) than the 74.5 young trees per hectare in an area without roots (this corresponds to 134.25 m² available surface per tree). As shown in Figs. 1 and

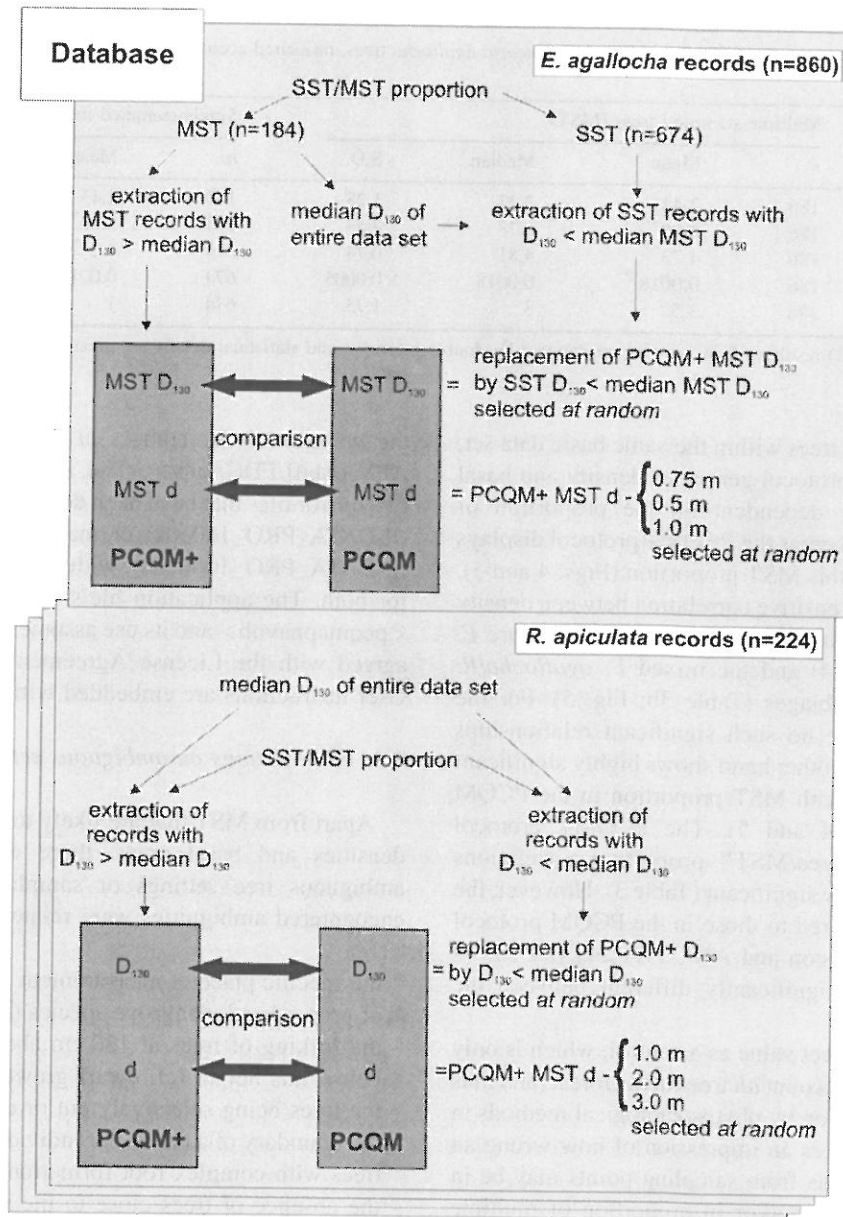


Fig. 3. Protocol for analysing the dependence of density and basal area calculations on stem position within multiple-stemmed trees of *Excoecaria agallocha* and *Rhizophora mucronata*. The comparison, based on real data, is between closer thinner stems (PCQM) and central thicker stems (PCQM+). Next to the database of multiple-stemmed trees (MST) also that of single-stemmed trees (SST) was used, because when simply recording the 'closest' stem (PCQM) it does not matter whether the tree was single- or multiple-stemmed. The PCQM+ distance d (between the sampling point and the nearest individual), as measured in the field, was subtracted by a randomised but realistic species-specific value to simulate a shorter distance (PCQM), and the PCQM+ stem diameter at 130 cm above the floor D_{130} was replaced by another as shown to simulate the thinner diameter. See text for more details on procedure.

2D this may bias the outcome of the PCQM, since a central, thick, adult stem of *Rhizophora* will always end up being surrounded by thinner young stems that were entangled by the prop root complex.

3.2. Differences between single- and multiple-stemmed *E. agallocha* trees

The confrontation of physiognomic and structural attributes between single-stemmed and multiple-stemmed trees (Table 2) indicated that there were no significant differences in the

sampling point to nearest individual distance ($t = 0.189$; d.f. = 334; n.s.), but that the differences in D_{130} ($t = -6.237$; d.f. = 343; $p < 0.001$), basal area ($t = -7.329$; d.f. = 347; $p < 0.001$) and height ($t = -8.043$; d.f. = 376; $p < 0.001$) were highly significant.

3.3. Dependence of silvometric parameter calculations on stem position within multiple-stemmed trees

In comparing pair-wise PCQM analysis based on closer thinner stems and PCQM+ analysis based on central thicker

Table 2
Descriptive statistics for multiple-stemmed and single-stemmed *Excoecaria agallocha* trees, measured according to the protocol indicated in the text (see Section 2.2.2)

	Multiple-stemmed trees (MST)				Single-stemmed trees (SST)			
	<i>n</i>	Mean	Median	S.D.	<i>n</i>	Mean	Median	S.D.
Distance <i>d</i> (m)	186	2.41	2.33	1.28	173	2.43	2.26	1.56
Diameter <i>D</i> ₁₃₀ (cm)	186	6.99**	6.78	2.53	674	5.63**	5.09	3.01
Height <i>h</i> (m)	186	4.73**	4.81	0.74	674	4.2**	4.25	0.97
Basal area <i>Ba</i> (m ² /0.1 ha)	186	0.0018**	0.0018	0.0005	674	0.0015**	0.0014	0.0006
Number of stems	186	3.5	3	1.75	674	1	1	0

Significant differences ($p < 0.001$) resulting from a *t*-test are denoted by double asterisks, and statistical details are given in the text.

stems in multiple stemmed trees within the same basic data set, we found that the PCQM protocol generates density and basal area data that are highly dependent on the proportion of multiple-stemmed trees, whereas the PCQM+ protocol displays more an independency on this MST proportion (Figs. 4 and 5). In the PCQM protocol, the positive correlation between density and MST proportion is highly significant for both the pure *E. agallocha* (Table 3a; Fig. 4) and the mixed *E. agallocha*/R. *apiculata* mangrove assemblages (Table 3b; Fig. 5). For the PCQM+ protocol there are no such significant relationships (Table 3). Basal area on the other hand shows highly significant and negative correlations with MST proportion in the PCQM protocol (Table 3; Figs. 4 and 5). The PCQM+ protocol generates positive 'basal area/MST'- proportion correlations that are moderately to highly significant (Table 3). However, the trend is rather weak compared to those in the PCQM protocol (Figs. 4 and 5), and regression and ANCOVA analysis shows that all comparisons are significantly different between the protocols (Table 4).

In absence of a true correct value as a control, which is only obtained when taking into account *all* trees in the forest (and thus on adopting no approximation by phytosociological methods in sampling points), Fig. 6 gives an impression of how wrong an approximation measurements from sampling points may be in forests that differ in density and/or in proportion of multiple stemmed trees. Forests consisting of MST only, in which the trees are sparsely spread, will have a majority of sampling points that will over-estimate the density and underestimate the basal area (Fig. 6, lower left rectangle). The figure indicates that as density changes, and as the proportion of multiple-stemmed trees decreases (and that of single-stemmed trees increases), the factors by which density and basal area are over- or underestimated change as well, and eventually become equal to 1.

3.4. PCQM-related silvimetric parameter computations

One of the end products of this paper is P-DATA PRO, a Microsoft® Excel Workbook application with formulae that automatically calculate all PCQM-related parameters discussed in this paper (Eq. 1 to 10) when basic data are filled out. It is the first automated interface that processes PCQM data (regardless of the forest ecosystem), and it is freely available in Appendix C to users who may want to apply it or develop it further (see license agreement). Possible future versions will be posted on

the website of the authors at URL <<http://www.vub.ac.be/APNA/staff/FDG/pub/>>. The above web directory contains two mirror files that have been developed to treat maximum 100 (P-DATA_PRO_100.xls) or maximum 1000 sampling points (P-DATA_PRO_1000.xls), with a maximum of 30 tree species for both. The application file's sharing code for either file is <pcqmapnavub> and its use assumes that the user has read and agreed with the License Agreement (see also Appendix A). User instructions are embedded within the application file.

3.5. Observations on ambiguous settings for measurement

Apart from MST that are likely to generate erroneous forest densities and basal areas, there were a number of other ambiguous tree settings or sampling situations. The most encountered ambiguities were related to:

- the specific place of measurement for the *D*₁₃₀ within a stem of prop-rooted mangrove species (*Rhizophora* in particular);
- the forking of trees at 130 cm above the floor, or above or below this height (cf. dwarf growth);
- the trees being selectively cut or dead;
- the boundary of a particular individual (particular for MST or trees with complex root formations);
- the absence of trees close to the sampling points in sparse assemblages;
- the consideration of a same tree by two or more sampling points in sparse assemblages;
- the validation of remotely sensed imagery using the PCQM.

The clarification and remediation of the above situations is given in Section 4.

4. Discussion

4.1. Are there problematic settings for applying the PCQM?

The problematic settings that were introduced theoretically at the beginning of this paper indeed exist in practice. The results of the comparison of the spatial distribution of young trees with respect to the root complex of *Rhizophora* species suggest that the entanglement of propagules by the root complex of *Rhizophora* does significantly influence the

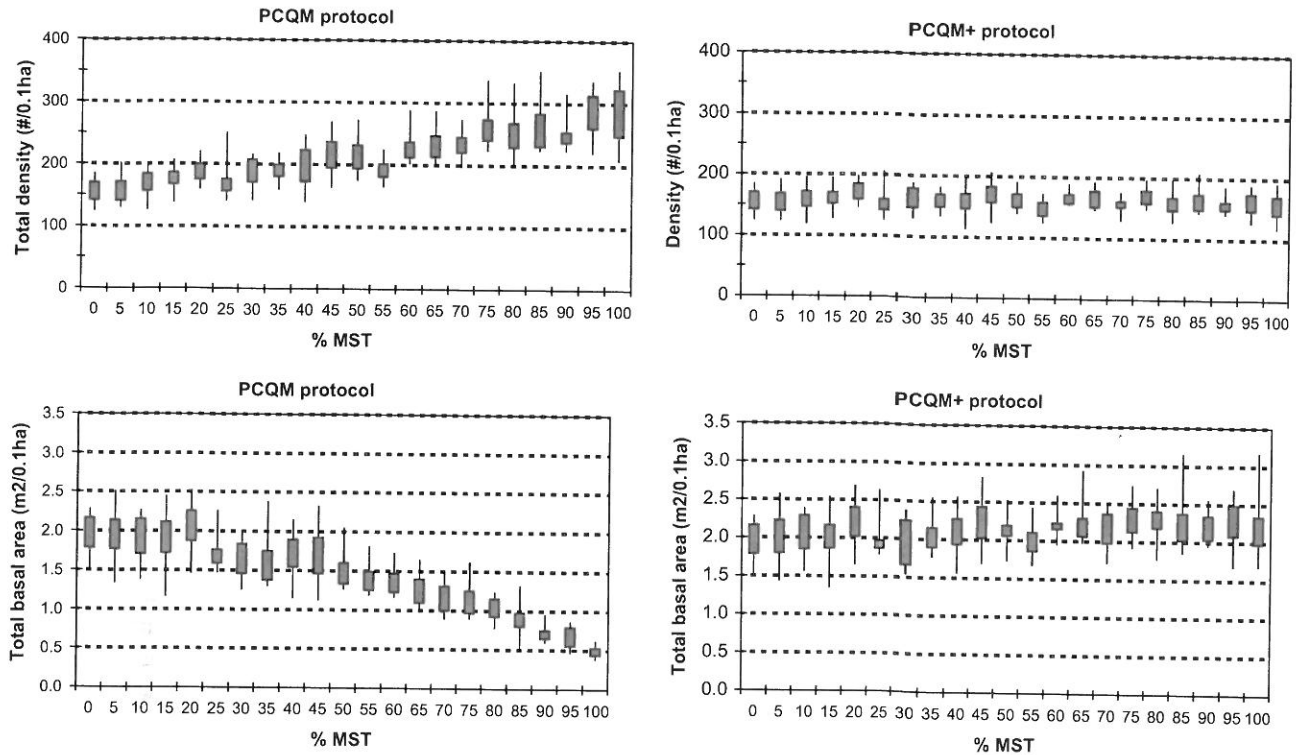


Fig. 4. Box plots showing the total absolute density and basal area of the *Excoecaria agallocha* mangrove assemblage in function of the proportion of multiple-stemmed trees (MST), as compiled by the PCQM protocol and by the PCQM+ protocol. The boxes represent the data between the 25th and the 75th percentile whereas the lines extend to the minimum and maximum values. Statistics for the observed trends are given in Table 4.

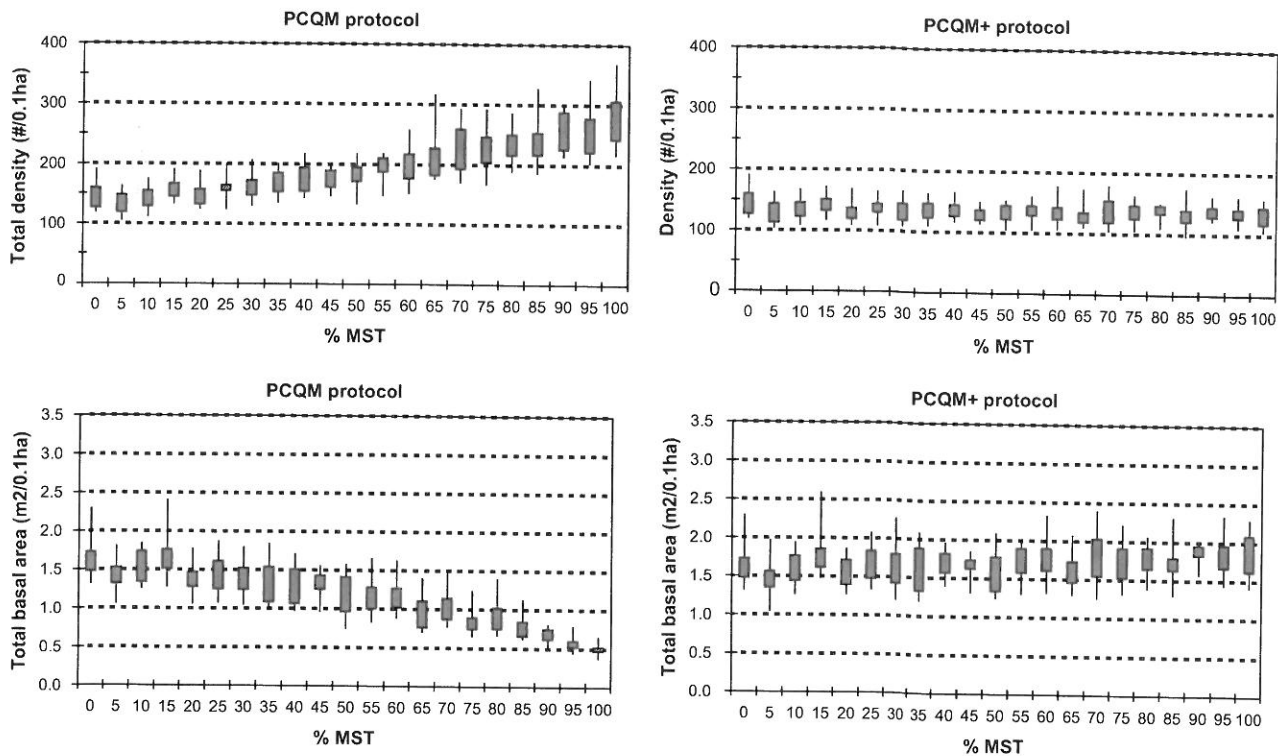


Fig. 5. Box plots showing the total absolute density and basal area of the *Excoecaria agallocha*/*Rhizophora apiculata* mixed mangrove assemblage (in 3:1 proportions, respectively) in function of the proportion of multiple-stemmed trees (MST), as compiled by the PCQM protocol and by the PCQM+ protocol. The boxes represent the data between the 25th and the 75th percentile whereas the lines extend to the minimum and maximum values. The density and the basal area for each of the two species is not shown graphically as they display the same trends, but their statistics are given in Table 4.

Table 3

Correlation statistics for the relationship between the protocol and the MST proportion for the pure *Excoecaria agallocha* (a) and the mixed *Excoecaria agallocha*/*Rhizophora apiculata* mangrove assemblages (b)

	PCQM protocol	PCQM + protocol
(a) Pure <i>E. agallocha</i> mangrove assemblage		
Total density correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	0.96	0.03
<i>t</i>	15.622**	0.115
Total basal area correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	–0.97	0.71
<i>t</i>	–17.148**	4.300**
(b) Mixed <i>E. agallocha</i> / <i>R. apiculata</i> mangrove assemblage		
Total density correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	0.98	–0.07
<i>t</i>	22.091**	–0.320
Total basal area correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	–0.97	0.77
<i>t</i>	–16.644**	5.210**
<i>E. agallocha</i> density correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	0.97	–0.27
<i>t</i>	17.465**	–1.211
<i>E. agallocha</i> basal area correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	–0.95	0.58
<i>t</i>	–14.003**	3.046*
<i>R. apiculata</i> density correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	0.96	0.06
<i>t</i>	15.525**	0.263
<i>R. apiculata</i> basal area correlations with % MST		
<i>n</i>	21	21
<i>r</i> ²	–0.96	0.89
<i>t</i>	–14.458**	8.670**

Graphical representations for total densities and total basal areas are given in Figs. 4 and 5. The correlation was tested using a *t*-test and asterisks denote a significant relationships (**p* < 0.01; ***p* < 0.001). Silvometric parameters that displayed significant relationships for *both* protocols were further analysed using regression and analysis of covariance (Table 4).

intended *at random* choice of stems in nearest individual or nearest neighbour distance methods, such as the Point-Centred Quarter Method. Since one or few adult trees attract many young trees – this is a process that may be direct or indirect through the entanglement of debris first (Stieglitz and Ridd, 2001; Krauss et al., 2005), which is affected by the tidal amplitude, it is virtually impossible to attribute an equal chance of being selected to each adult stem, and therefore complete randomness cannot be reached. As a result the possibility exists for a closest tree, not only to be younger, but also to be of a different species than the species with the complex root system. This is one reason to focus on the thicker central stems of multiple-stemmed trees.

Our results also indicate that MST and SST have significantly different physiognomic characteristics, such as

*D*₁₃₀, basal area and height, which is another incentive to differentiate between these individuals in the field. The distance from an *at random* sampling point to the nearest stem sensu stricto is however independent from the tree type, which is also within the logic of randomness.

The main reason for differentiating between the closer and central stems of MST is the potential overestimation of density (because the PCQM systematically considers a stem standing closer to the sampling point than the central stem), and the potential underestimation of basal area (because the PCQM systematically considers a stem being thinner than the central stem). Dealing with this problem necessitates the adaptation of the PCQM protocol in favour of a PCQM+ protocol that is not sensitive to such MST-related problems.

4.2. The PCQM+ protocol

Even though we do not have a basis for comparison to the true values of density and basal area in our study site, it is rather worrying that the classical PCQM protocol is significantly varying with MST proportion for forests with a constant density. The bottom row of situations in Fig. 6 indeed suggests that this should not be the case if one consistently considers the central stem of an MST. In fact, it is exactly this robustness that our PCQM+ protocol displays, and that has been demonstrated statistically (Figs. 4 and 5; Tables 2 and 3). Even if there would be a deviation from true values, this error would be systematic and constant. Also the constant variation in the results displayed by the PCQM+ protocol (summarised as boxes in Figs. 4 and 5), as opposed to the changing variation in the results displayed by the PCQM protocol, is indicative for its reliability. The fact that the basal area is less affected by the tree type (SST or MST) is also reassuring for the establishment of allometric relationships based on *D*₁₃₀ such as biomass (Baskerville, 1972; Suzuki and Tagawa, 1983; Woodroffe, 1985; Putz and Chan, 1986; Clough and Scott, 1989; Amarasinghe and Balasubramaniam, 1992a,b; Tam et al., 1995; Slim et al., 1996; Clough et al., 1997; Fromard et al., 1998; Komiyama et al., 2000; Ong et al., 2004). The same is true for the study of density or *D*₁₃₀-related processes such as competition (Nissen and Midmore, 2002), succession (Smith III, 1992; Lugo, 1997; Duke, 2001), impact assessment (Imbert et al., 1996, 1998; Dahdouh-Guebas et al., 2002), or for processes that may be reflected by tree density or *D*₁₃₀, such as hydrological changes (Ernst and Brooks, 2003; Dahdouh-Guebas et al., 2005b).

Ideally, the density and basal area, which were compiled and calculated from field data that were collected by sampling points approximating the true values, should be compared with the true values themselves. However, obtaining the true values is only possible if all trees in a forest are counted and their *D*₁₃₀, height, and so forth are measured, which is highly time-consuming and not at all cost-effective. The remaining challenge for any phytosociological or vegetational survey method is to compare their approximate results between the true values of forests with differing compositions, physiognomies or vegetation structures (species-poor versus species-

Table 4
Regression and analysis of variance (ANCOVA) statistics for the differential correlations for the relationship between basal area and MST proportion in the two protocols

	PCQM protocol	PCQM+ protocol
(a) Pure <i>E. agallocha</i> mangrove assemblage		
Total basal area		
<i>n</i>	21	21
d.f.	19	19
<i>r</i>	−0.97	0.74
<i>a</i>	2.152	1.987
<i>b</i>	−0.015	0.003
b_{PCQM} vs. b_{PCQM+}	$t = 17.154$; d.f. = 38; $p < 0.01$	
r_{PCQM} vs. r_{PCQM+}	$\chi^2 = 17.154$; d.f. = 38; $p < 0.01$	
ANCOVA	Variance between treatments = 0.714 Residual variance = 0.091 $F = 62.172$; d.f. = 1 & 39; $p < 0.001$	
Confrontation between elevations	$t = 7.885$; d.f. = 39; $p < 0.01$	
(b) Mixed <i>E. agallocha</i> / <i>R. apiculata</i> mangrove assemblage		
Total basal area		
<i>n</i>	21	21
d.f.	19	19
<i>r</i>	−0.97	0.78
<i>a</i>	1.648	1.561
<i>b</i>	−0.010	0.003
b_{PCQM} vs. b_{PCQM+}	$t = 16.463$; d.f. = 38; $p < 0.01$	
r_{PCQM} vs. r_{PCQM+}	$\chi^2 = 87.405$; d.f. = 38; $p < 0.01$	
ANCOVA	Variance between treatments = 0.562 Residual variance = 0.067 $F = 70.318$; d.f. = 1 & 39; $p < 0.001$	
Confrontation between elevations	$t = 8.386$; d.f. = 39; $p < 0.01$	
<i>E. agallocha</i> basal area		
<i>n</i>	21	21
d.f.	19	19
<i>r</i>	−0.95	0.534
<i>a</i>	1.35	1.238
<i>b</i>	0.001	0.002
b_{PCQM} vs. b_{PCQM+}	$t = 11.479$; d.f. = 38; $p < 0.01$	
r_{PCQM} vs. r_{PCQM+}	$\chi^2 = 52.505$; d.f. = 38; $p < 0.01$	
ANCOVA	Variance between treatments = 0.414 Residual variance = 0.058 $F = 51.218$; d.f. = 1 & 39; $p < 0.001$	
Confrontation between elevations	$t = 7.157$; d.f. = 39; $p < 0.01$	
Total basal area		
<i>n</i>	21	21
d.f.	19	19
<i>r</i>	−0.89	0.832
<i>a</i>	0.334	0.279
<i>b</i>	−0.002	0.001
b_{PCQM} vs. b_{PCQM+}	$t = 10.816$; d.f. = 38; $p < 0.01$	
r_{PCQM} vs. r_{PCQM+}	$\chi^2 = 62.32$; d.f. = 38; $p < 0.01$	
ANCOVA	Variance between treatments = 0.124 Residual variance = 0.02 $F = 38.316$; d.f. = 1 & 39; $p < 0.001$	
Confrontation between elevations	$t = 6.19$; d.f. = 39; $p < 0.01$	

Statistics are given for the pure *Excoecaria agallocha* (a) and the mixed *Excoecaria agallocha*/*Rhizophora apiculata* mangrove assemblages (b). *a*, intercept; *b*, slope; *r*, correlation.

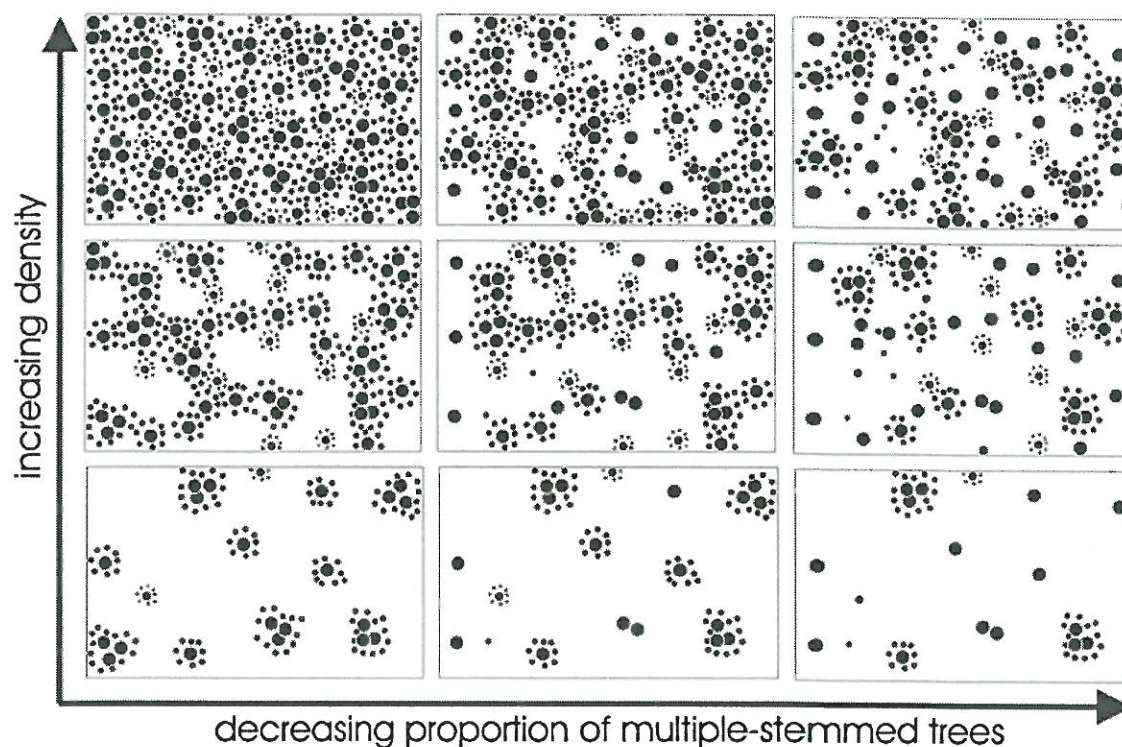


Fig. 6. Forests with differing proportions of multiple-stemmed trees (columns) and differing densities (rows). A multiple-stemmed tree (MST) such as *Excoecaria agallocha* (Fig. 1), is typically represented by large circles (thicker central stems) surrounded by smaller circles (thinner stems). A single-stemmed tree (SST) is represented by a small or large circle without surrounding stems. Note from the vegetation structures (and from *at random* or transect sampling points that are to be placed amongst the trees) that, if a classical PCQM protocol is adopted (measurement of the closest stem), over-estimation of density and under-estimation of basal area is most problematic in the lower left situation (sparsely distributed MST only), and decreases with increasing densities and decreasing MST proportions. Note on the other hand that a PCQM+ protocol (measurement of the central stems) is virtually independent of the density and the proportion of multiple-stemmed trees (see also Figs. 4 and 5 with their statistics in Tables 2 and 3).

rich, well developed versus dwarf growth, zoned versus patchy, dense versus sparse, evenly dispersed versus aggregated).

4.3. Other problematic settings for measurement and their possible solutions

It seems that there is little opportunity to follow a diameter or distance measurement by the book in the classical PCQM protocol, but each tree should be approached separately and the researcher should adopt a 'best professional consistency'. However, this is not evident when the results from different researchers are to be compared, not even when the used entities are well defined and highly standardized (cf. Brokaw and Thompson, 2000). In the light of the description of the PCQM+ protocol in this paper, we would like to include a number of suggestions to streamline diameter measurements and solutions to ambiguous settings for sampling points or measurements.

4.3.1. Specific place and height for diameter measurement

Next to the problem of the choice between different stems within an MST, there is also an ambiguity in the exact location of the measurement of the D_{130} within a stem, which also influences the basal area. The variation in basal area or biomass that can occur for measurements of the tree diameter taken at different heights along a mangrove stem highlights the need for

the establishment of more transparent procedures in measuring this diameter, particularly in *Rhizophora* species. Brokaw and Thompson (2000) demonstrated on more conventional tree architectures in temperate forests that diameter measurements differing 10 cm in a height along stems, generate incomparable biomass results.

Considering that scientists have referred to the height in DBH, although well defined and standardised at 130 cm, as any height between 120 cm and 160 cm above the floor (loc. cit.; Martin, 2004), Brokaw and Thompson (2000) suggested to do away with the term DBH in favour of D_x (with 'x' denoting the exact height along the stem for the diameter measurement). However, in mangrove trees this may not be enough to unambiguously point out a place to measure the diameter (Fig. 2).

One of the suggestions that has been made for the *Rhizophora* genus, some species of which usually contain prop roots at 130 cm above the floor, is to measure the diameter 30 cm above the upper root. However, some upper roots are well established in the mangrove mud, while others have just started forming (Fig. 2D). In addition, some roots are formed from within the canopy (Fig. 2A and B). We suggest that only roots originating from the central stem and touching the mangrove soil or permanent water body are considered, when pointing out the 'upper root'.

The single stem (at floor height) of some mangrove trees is splitting at 130 cm above the floor, or has already split into two or more stems. We follow Cintrón and Schaeffer Novelli (1984) and suggest that in no case the thicker part near splitting or branching positions (or rooting positions for that matter) are considered for measuring the diameter. We also emphasize the use of common sense to choose one of two options (depending in part of the objective of the study): measuring the diameter below the split, or measuring it 30 cm above the split and averaging two or more stem diameters. We strongly oppose to measure the diameter at a standard distance below a split because some mangrove trees typically split very low. This is the case for large areas of *C. tagal* (Perr.) C.B. Robinson in Kenya splitting at <30 cm above the floor, for *Avicennia marina* (Forsk.) Vierh. displaying dwarf-growth (Dahdouh-Guebas et al., 2004a) and branching below a height of 1 m, or for *Avicennia germinans* (L.) Stearn on tidal islands at its biogeographical limit that are growing upward for about 1 m and then develop horizontally (Dahdouh-Guebas and Koedam, 2001).

We stated in Section 2 that by using the term ' D_{130} ' we intend a measurement at 130 cm above the floor and along the stem, because some trees may be crooked or developing sideways rather than in height (loc. cit.). The diameter of a tree with a horizontally protruding stem should thus be measured 130 cm along the stem, even if this is less than 130 cm above the floor. This is often the case for *L. racemosa* Willd. or *L. littorea* (Jack) Voigt in Sri Lanka, and for the MST of *E. agallocha* (Fig. 1A). There are also situations thinkable with unlevel ground in which the orientation of the stem and the topography play a role, but the discussion of these is beyond the scope of this paper, and they have been summarized by Dallmeier (1992).

4.3.2. Dead or partially cut trees

Mangroves are of subsistence use for local inhabitants, who have species preferences for certain uses (Bandaranayake, 1998; Ewel et al., 1998; Dahdouh-Guebas et al., 2000a; Walters, 2005). This may result in selective logging of trees, but also in the selective removal of tree parts. This in turn may strongly influence the architecture of a tree, the physiognomy of vegetation assemblages, and the species composition. *B. gymnorhiza*, which has usually a single stem on the forest floor, is often found partially cut at a particular height, and as a result displays newly grown stems. Another example is from Kairo et al. (2002b), who reported the presence of low quality, crooked, thinner *Rhizophora mucronata* Lamk. trunks, as opposed to high quality, straight, thick, trunks, in a Kenyan site where this species is cut for house construction. They also reported shifts in species dominance as a result of the same (loc. cit.). Follows that selective removal of trees or tree parts influences the tree nearest to a sampling point, the height of 130 cm above the floor or along a stem, and the diameter of the stem, and as elaborated in the following section, the boundaries of an MST. Another possible consequence of selective removal of tree parts is that the tree dies. In both cases the trees or the tree

parts should only be considered if the study is interested in the natural growth and regeneration status of trees (thus considering the stem diameter where the tree was cut, or disregarding die-off due to cutting), or if the purpose of the study is to assess the wood resource exploitable in its dead form (e.g., subsistence based firewood). However, if the purpose of the study is to assess the wood resource exploitable for construction, the tree trivially merits no further consideration.

4.3.3. Boundary of a single-stemmed or a multiple-stemmed tree

The suggestion made in the PCQM+ protocol to measure the central stems of MST, must be assessed case by case using a 'best professional consistency' when it comes to *Rhizophora* species. The representatives of this genus are typically linked through complex root systems. In some cases individual trees (whether or not multiple-stemmed) can be distinguished clearly. In other cases, however, many stems may seem to originate from a single root complex covering a surface of >25 m². If the PCQ-Method were applied according to the book ('PCQM-protocol'), a tree with a root complex on which a total of 10 stems originate would be considered only once. However, if the root connections break, as it frequently happens, there is no more reason to consider it a single tree, and the stems would be considered as separate trees. Apart from the fact that it is very tedious to untangle the tree connections, this would obviously give rise to a distance and a tree diameter that are not always correct, and, even worse, not always consistent. We suggest that in such a situation, stems that are not attached directly to each other within a certain distance limit of 3 m, should be considered separate individuals, even if they are clearly connected indirectly through the root complex. The underlying ecological justification for this is that each of these stems is connected to enough roots to assure the ability to further develop if the root connections with other stems are broken.

4.3.4. Distance limits

It is most advisable to make sure that each quadrant in the field contains a tree, whatever its distance, instead of adopting a distance limit, as the latter will need to be corrected in a later phase (e.g., Verheyden, 1997). The rationale for using a distance limit is that some may be interested in describing the local density (near the sampling points on a transect) rather than the entire density of a forest. Since species richness and area covered are not related in the PCQM (Cunningham, 2001), and since the absence of close-by species in an open vegetation assemblage with very sparsely distributed individuals is only logic (Dahdouh-Guebas et al., 2000b; Verheyden et al., 2002; Dahdouh-Guebas et al., 2004b), a consistent distance limit for the sampling point to nearest individual distance may be more appropriate, than the alternative, i.e. the consideration of a same individual twice. Adopting a distance limit will therefore result in some quadrants containing no tree. Although in the present study we did not adopt such a distance limit, nor did we consider a same individual more than once (see Section 2), we

do not oppose its use for sparse vegetation in the light of the above explanation. However, a distance correction factor should be applied when calculating the density, so that density is only calculated based on quadrants that did contain a tree. We suggest adopting the following formula for the calculation of total assemblage density corrected for empty quadrants (De') under the above circumstances:

$$\text{De' (in stems/0.1 ha)} = \frac{1}{(\sum_{j=1}^n d_j/n)^2} \times \frac{q_n}{q_t},$$

(corrected density) (10)

where d_j is the sampling point to nearest tree distance for tree j ; n , number of trees sampled; q_n , number of quadrants containing a tree; q_t , total number of quadrants, $4 \times$ number of sampling points.

We also recommend more research effort in evaluating the effect of considering an individual more than once in PCQM calculations. Cottam and Curtis (1956) did not use any method of mutual exclusion in the location of sampling points, but Cintrón and Schaeffer Novelli (1984) indicated the selection of any tree twice as a limitation to the PCQ-Method. Although in a preliminary analysis Dahdouh-Guebas (2001) did not find evidence for negative effects from this, at present there is not enough empirical evidence to determine whether or not it is significantly affecting the accuracy of density calculations.

4.3.5. Remote sensing validation through the PCQM

The PCQM can be used as a ground-truth method for remote sensing studies in combinatory investigations (e.g., when studying spatio-temporal dynamics and where mapping is combined with in-depth characterisation of vegetation layers). The visualisation of vegetation distribution in the field is very straightforward in geographical information systems (GIS), and this tool offers unique methodological combinations (Dahdouh-Guebas et al., 2000b, 2004b; Verheyden et al., 2002). However, there are two important considerations that must be made when adopting PCQM as a remote sensing ground-truth method.

The first is that remote sensing provides information about the canopy of a vegetation, whereas PCQM provides information about the stems on the floor. A lack of correspondence between both may lead to the erroneous interpretation that image classifications are inaccurate. This is for instance the case where a single large tree consists of multiple stems on the floor, where a continuous canopy, however small, may comprise several tree crowns, each with their own stem, or where overtopping of one tree species by another occurs. The latter situation is the case in many forest types world-wide. In seaward mangrove fringes it occurs when sparse, tall *A. marina* trees are overtopping dense, slightly smaller *R. mucronata* trees (Dahdouh-Guebas et al., 2004b). We suggest that where the PCQM is used as a ground-truth method, the surveyor indicates in the field whether or not the sampled trees are canopy representatives. Where this is not the case, the surveyor should also consider the canopy trees either

quantitatively (by also applying the PCQM to the nearest canopy individual) or qualitatively (by estimating the percentage cover for the canopy trees in a quadrat in each of the PCQM quadrants), the latter of which may be most practical.

The second consideration is that the PCQM provides a distance to the nearest tree per quadrant, but within the 0 to 90° quadrant there is no indication as to the direction in which the tree is located. When confronting the distance with the remotely sensed image in a forest, it may be impossible to distinguish between the different crowns that correspond to that distance. This may be problematic in forests with a heterogeneous vegetation structure, or when the aim is to pinpoint individuals on the image (Dahdouh-Guebas et al., 2005a). Image classification may of course help to distinguish between trees based on spectral characteristics, but may not be able to resolve all ambiguities (loc. cit.). Therefore we suggest to indicate the angle with respect to the transect direction for the nearest tree in each quadrant. Alternatively, approximate angle classes can be used (e.g., 0–30°, 30–60°, 60–90°) to reduce the number of possible crowns that correspond to the sampling-point-to-nearest-individual distance.

Finally, it must be emphasised once more that the above combinatory approach is useful when combining mapping with an in-depth study of the vegetation layers, the latter of which is faster using a PCQM approach. However, it is counter-advised to use PCQM for pure ground-truthing. Plot-based or visual observation-based approaches are more advantageous if the sole aim is to ground-truth the canopy vegetation for air-borne or space-borne image analysis purposes.

4.4. Advantages and disadvantages of the PCQM

Although it is sometimes stated that the PCQM is a labour-intensive method (Campbell, 1989), we would like to commend the fast and easy way in which it can be applied. Compared to plot-based methods, which are both labour-intensive within a sampling and within the generation of a statistical relevant number of samples, the PCQM is proceeding faster from one sampling point to another. Per sampling point it considers four different trees, unlike the distance measurements in other plot-less methods such as the nearest individual method, the nearest neighbour method, or the random pairs method, which are limited to one per sampling point (Cottam and Curtis, 1956). Contrary to the use of plot-based methods, the PCQM does not cover an exact area each time. The consequence is that species richness cannot be related to area sampled (Cunningham, 2001). However, the use of many sampling points along line transects covering the width of the vegetation, which is also how we suggest applying the PCQM, should remediate this problem. When choosing a sampling design, one should also consider the purpose of the study (e.g., is it a descriptive silvicultural study, or does it aim at linking observed patterns in vegetation to environmental factors?), the previous information gathered, and evaluate the best sampling design (random, systematic, stratified) in the light of the spatial structure present. The sound assessment of these may greatly enhance the

reliability of the analysis of ecological field surveys (Legendre et al., 2002).

In studies combining aerial photography as a remote sensing method and PCQM as the ground-truth method, quantitative overlay analysis has shown that the PCQM does provide the same species data as the imagery (Dahdouh-Guebas et al., 2000b; Verheyden et al., 2002). This brings us back to the important advantage of the PCQM as a ground-truth method for remote sensing (RS) studies in combination with vegetation analysis, and the possibility of a readily interpretable visualization in GIS-environment. Apart from this PCQM-RS&GIS combinatory approach, another unique methodological combination is between PCQM and ordination analysis (Dahdouh-Guebas et al., 2002). Retrospective-predictive studies regarding vegetation structure dynamics carried out using RS and GIS, can actually be strengthened by field data about different age classes using the PCQM for sampling (Dahdouh-Guebas and Koedam, 2002). The PCQM transects along which adult trees (and canopy trees) have been sampled, can be used to study understory characteristics (by applying the PCQM to the young tree vegetation layer), and even the juvenile vegetation layer (using plot-based propagule counts around the sampling points where adult and young trees are measured using the PCQM). Abundances per sampling point (ranging between 0 and 4 for PCQM sampling points) and per vegetation layer can then be used as a matrix input for ordination analysis. Dahdouh-Guebas and Koedam (2002) and Dahdouh-Guebas et al. (2004b) have reported changes in mangrove vegetation structure using these two complementary combinatory approaches in which the PCQM occupies a central importance. Studying spatio-temporal dynamics in this way allows for predictions based on vegetation history, with retrospection based on sequential remote sensing, and prediction based on vegetation layers of different age.

5. Conclusions

This paper deals with a methodological discussion about the Point-Centred Quarter Method, used in the domain of structural studies for forest ecosystems. Although unrelated to forest type, we applied this method to a mangrove forest data set, characterised by structural parameters as diameters, heights,

density, basal area, etc. ... Single and multiple-stemmed trees are taken into account.

Our core results indicate that the classical PCQM protocol generates density and basal area results that are much less robust than those obtained with the introduced PCQM+ protocol, which does not consider the tree nearest to a sampling point, but the central stem of aggregating trees. The paper includes a rigorous description of the improvements to the method (PCQM+ protocol), and elaborates on the solutions to other common problems related to ambiguous settings for the consideration of stems or the measurement of their diameter. Such ambiguous settings are unrelated to forest type and may include problematic root systems, split trunks, dwarf growth architecture, horizontally developing stems, boundary of an individual in multiple-stemmed trees, selectively cut trees or tree parts, very sparse assemblages, use of PCQM for remote sensing ground-truth and for studying understory characteristics. A comprehensive appendix matches the specific solutions to specific problems.

Finally, our paper is also accompanied by the first interface that automatically processes standard PCQM-related data (not restricted to mangroves) to generate common silvometric or forestry parameters elaborated in this paper. This application is provided in Supplementary Data.

Acknowledgements

We are very grateful to the staff of the Small Fishers Federation of Lanka (Pambala-Kakkapalliya, Sri Lanka), in particular Mr. Anuradha Wickramasinghe (Director), and Mr. Daglas W.N. Thisera (Coordinator Mangrove Conservation and Education, SFFL) for practical help in the field, to all our students and to our partners from the University of Ruhuna for support in the wider mangrove research framework. The first author is a Postdoctoral Researcher of the Fund for Scientific Research (FWO-Vlaanderen). The research was also financed by the European Commission (Contract EBR IC18-CT98-0295), and with a specialisation fellowship of the Institute for the Promotion of Innovation by Science and Technology in Flanders (IWT). We thank two anonymous reviewers for their constructive comments.

Appendix A. PCQM Data Processing (P-DATA PRO version 1.04) and its License Agreement

P-DATA PRO or Point-Centred Quarter Method Data Processing is a Microsoft® Excel-based Workbook application that constitutes an integral part of this paper. P-DATA PRO is the first interface that calculates different forestry characteristics based on fieldwork using the Point-Centred Quarter Method (PCQM-protocol or PCQM+ protocol) for maximum 30 species and 100 sampling points. There is also a mirror version available that can process up to 1000 sampling points. Both files can be downloaded freely from the following websites, the action of which assumes agreement with the License Agreement below:

Publisher website:

P-DATA PRO 100: Appendix C

P-DATA PRO 1000: Appendix C

Website Vrije Universiteit Brussel:

P-DATA PRO 100: http://www.vub.ac.be/APNA/staff/FDG/pub/P-DATA_PRO_100.xls

P-DATA PRO 1000: http://www.vub.ac.be/APNA/staff/FDG/pub/P-DATA_PRO_1000.xls

Appendix A (Continued)

The version of the application at the time of publication is version 1.04 and is available from the publisher's website. Possible future versions will be made available through the corresponding authors' website at Vrije Universiteit Brussel URL <<http://www.vub.ac.be/APNA/staff/FDG/pub/pub.html>>.

P-DATA PRO LICENSE AGREEMENT

The user acknowledges that the use of the software application is subject to the terms and conditions of this license agreement. Use of the file sharing code to activate the file confirms this acknowledgement.

The user may only use the software application for the purposes of calculating the forestry variables and parameters provided in the file and described in the peer-reviewed scientific paper referenced as '**Dahdouh-Guebas, F. & N. Koedam, 2006. Empirical estimate of the reliability of the use of the Point-Centred Quarter Method (PCQM): solutions to ambiguous field situations and description of the PCQM+ protocol. *Forest Ecology and Management* 228, 1–18.**', and provided that complete citation is given to the above paper. The user is not allowed to use the software application for any other purposes.

The software application and the associated intellectual property rights are the ownership of the Vrije Universiteit Brussel. The software application is protected by copyright. The user is not allowed to change or further develop the software application, for commercial or other purposes, without the prior written and signed agreement of the corresponding author at Vrije Universiteit Brussel. The corresponding author's contact details are : Farid Dahdouh-Guebas, Biocomplexity Research Team c/o Laboratory of General Botany and Nature Management, Mangrove Management Group, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussel, Belgium. Tel. + 32 (02) 629.34.22, Tel. & Fax. + 32 (02) 629.34.13, E-mail : <fdahdouh@vub.ac.be>.

The software application can be downloaded free from the website of the publisher (Elsevier) and of the Vrije Universiteit Brussel. Future versions of the software application, if developed, will be available from the website of the Vrije Universiteit Brussel.

The software application is provided "AS IS", without any warranty of any kind, express or implied, including but not limited to the warranties of sufficiency, accuracy, use of application or performance, merchantability, fitness for a particular purpose, visible or hidden defaults or non-infringement of third party intellectual property rights.

In particular, the Vrije Universiteit Brussel cannot guarantee that the use of the software application will be error-free, free of bugs and free of any interruptions.

To the extent permitted by applicable law, in no case whatsoever will Vrije Universiteit Brussel be liable to you for any loss, damages, claims or costs, including but not limited to any consequential or indirect damages, any lost profits or lost savings, any damages resulting from business interruption, personal injury or claims by third parties.

This agreement will be governed by Belgian law. Any disputes, which cannot be settled amicably, shall be settled before the competent courts of Brussels.

Appendix B

Table synthesising the problems and our suggestions for solutions in the light of the PCQM+ protocol

Problem	Suggestion
Overestimation of density by systematically considering a stem standing closer than the central stem in forests with multiple-stemmed trees	<ul style="list-style-type: none"> Consider the central stem(s) instead of nearest stem Always take the distance to the approximate centre of the stem and not to its bark
Underestimation of basal area by systematically considering a stem being thinner than the central stem in forests with multiple-stemmed trees	<ul style="list-style-type: none"> Consider the central stem(s) instead of nearest stem
There is more than one central stem	<ul style="list-style-type: none"> Consider the centre of the multiple-stemmed formation for the distance, and consider the average of all central stems for the D_{130}^a
The root settings, to measure the tree diameter in <i>Rhizophora</i> 30 cm above the upper root, are ambiguous	<ul style="list-style-type: none"> Consider the upper root originating from the central stem and touching the mangrove soil or permanent water body
The stem is not growing upward and the height at which to measure the diameter (130 cm above the floor) is therefore ambiguous	<ul style="list-style-type: none"> Always measure 130 cm 'along the stem' rather than 'above the floor'
The stem splits and the setting to measure the diameter is therefore ambiguous	<ul style="list-style-type: none"> Never measure the diameter near the thicker part of a split Measure the diameter below the split, or measure it 30 cm above the split and average the two or more stem diameters^a In all cases measure the 130 cm 'along the stem', instead of 'above the floor'

Appendix B (Continued)

The tree has been partially cut by people

- If the purpose of the study is to investigate natural growth and regeneration status, then it can still be considered
- If the purpose of the study is to investigate exploitable wood resource, then it should not be considered

The tree is dead

- If there are signs that death was inflicted by man, and the purpose of the study is to investigate natural growth and regeneration status, then it can still be considered
- If the purpose of the study is to investigate exploitable wood and the tree can still serve the purpose (e.g., firewood), then it can still be considered
- If there are no signs that death was inflicted by man, or the purpose of the study is to investigate the wood resource exploitable for construction (or other applications that require healthy wood), then it should not be considered

It is not clear which particular stems of a *Rhizophora* species is part of the same individual

- Stems that are not attached directly to each other within a certain distance limit of 3 m, should be considered separate individuals, even if they are clearly connected indirectly through the root complex

The forest is so sparse that considering a tree in each quadrant often challenges the rule of thumb that no tree should be selected more than once

- Adopt an appropriate and consistent distance limit and list a quadrant as 'empty' if there is no tree within this limit
- Apply a distance correction as explained in the text when calculating the density

There is overtopping of one tree by another

- If sampled trees are not canopy representatives, consider the canopy trees either quantitatively (by also applying the PCQM to the nearest canopy individual) or qualitatively (by estimating the percentage cover for the canopy trees in a quadrat in each of the PCQM quadrants)

^a It is advisable to note down the diameters of all the stems considered in the field, and to perform averaging during the analysis phase.

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2005.10.076>.

References

- Amarasinghe, M.D., Balasubramaniam, S., 1992a. Net primary productivity of two mangrove forest stands on the northwestern coast of Sri Lanka. *Hydrobiologia* 247, 37–47.
- Amarasinghe, M.D., Balasubramaniam, S., 1992b. Structural properties of two types of mangrove stands on the northwestern coast of Sri Lanka. *Hydrobiologia* 247, 17–27.
- Bandaranayake, W.M., 1998. Traditional and medicinal uses of mangroves. *Mangroves and Salt Marshes* 2, 133–148.
- Baskerville, G.L., 1972. Use of logarithmic regression in the estimation of plant biomass. *Canadian Journal of Forestry* 2, 49–53.
- Bosire, J., Dahdouh-Guebas, F., Kairo, J.G., Koedam, N., 2003. Colonisation of non-planted mangrove species into restored mangrove stands in Gazi Bay Kenya. *Aquatic Botany* 76 (4), 267–279.
- Brokaw, N., Thompson, J., 2000. The H for DBH. *Forest Ecology and Management* 129, 89–91.
- Brandtberg, T., Walter, F., 1998. Automated delineation of individual tree crowns in high spatial resolution aerial images by multiple-scale analysis. *Machine Visions and Applications* 11, 64–73.
- Campbell, D.G., 1989. Quantitative inventory of tropical forests. In: Campbell, D.G., Hammond, H.D. (Eds.), *Floristic Inventory of Tropical Countries*. New York Botanical Garden, New York, USA, pp. 524–533.
- Cintrón, G., Schaeffer Novelli, Y., 1984. Methods for studying mangrove structure. In: Snedaker, S.C., Snedaker, J.G. (Eds.), *The Mangrove Ecosystem: Research Methods*. UNESCO, Paris, France, pp. 91–113.
- Clough, B.F., Scott, K., 1989. Allometric relationships for estimating above-ground biomass in six mangrove species. *Forest Ecology and Management* 27, 117–127.
- Clough, B.F., Dixon, P., Dalhaus, O., 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Australian Journal of Botany* 45, 1023–1031.
- Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37 (3), 451–460.
- Cunningham, A.B., 2001. *Applied Ethnobotany: People, Wild Plant Use and Conservation*. Earthscan Publications Ltd., London, U.K., 300 pp.
- Curtis, J.T., 1959. *The Vegetation of Wisconsin. An Ordination of Plant Communities*. University of Wisconsin Press, Madison, Wisconsin, USA.
- Dahdouh-Guebas, F., 2001. *Mangrove vegetation structure dynamics and regeneration*. PhD Sciences Dissertation, Vrije Universiteit Brussel, Brussels, Belgium, 317 pp.
- Dahdouh-Guebas, F., Koedam, N., 2001. Are the northernmost mangroves of West Africa viable?—A case study in Banc d'Arguin National Park. *Mauritania Hydrobiologia* 458, 241–253.
- Dahdouh-Guebas, F., Koedam, N., 2002. A synthesis of existent and potential mangrove vegetation structure dynamics from Kenyan, Sri Lankan and Mauritanian case-studies. *Meded. Zitt. K. Acad. Overzeese Wet./Bull. Séanc. Acad. R. Sci. Outre-Mer* 48 (4), 487–511.
- Dahdouh-Guebas, F., Mathenge, C., Kairo, J.G., Koedam, N., 2000a. Utilization of mangrove wood products around Mida Creek (Kenya) amongst subsistence and commercial users. *Economic Botany* 54 (4), 513–527.
- Dahdouh-Guebas, F., Verheyden, A., De Genst, W., Hettiarachchi, S., Koedam, N., 2000b. Four decade vegetation dynamics in Sri Lankan mangroves as detected from sequential aerial photography: a case study in Galle. *Bulletin of Marine Science* 67 (2), 741–759.
- Dahdouh-Guebas, F., Kairo, J.G., Jayatissa, L.P., Cannicci, S., Koedam, N., 2002. An ordination study to view vegetation structure dynamics in dis-

- turbed and undisturbed mangrove forests in Kenya and Sri Lanka. *Plant Ecology* 161 (1), 123–135.
- Dahdouh-Guebas, F., De Bondt, R., Abeysinghe, P.D., Kairo, J.G., Cannicci, S., Triest, L., Koedam, N., 2004a. Comparative study of the disjunct zonation pattern of the grey mangrove *Avicennia marina* (Forsk.) Vierh. in Gazi Bay (Kenya). *Bulletin of Marine Science* 74 (2), 237–252.
- Dahdouh-Guebas, F., Van Pottelbergh, I., Kairo, J.G., Cannicci, S., Koedam, N., 2004b. Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on retrospective remote sensing, social surveys, and distribution of trees. *Marine Ecology Progress Series* 272, 77–92.
- Dahdouh-Guebas, F., Van Hiel, E., Chan, J.C.-W., Jayatissa, L.P., Koedam, N., 2005a. Qualitative distinction of congeneric and introgressive mangrove species in mixed patchy forest assemblages using high spatial resolution remotely sensed imagery (IKONOS). *Systematics and Biodiversity* 2 (2), 113–119.
- Dahdouh-Guebas, F., Jayatissa, L.P., Sooriyarachchi, S., Lo Seen, D., Hettiarachchi, S., Koedam, N., 2005b. Transitions in ancient inland freshwater resource management in Sri Lanka affect biota and human populations in and around coastal lagoons. *Current Biology* 15 (6), 579–586.
- Dallmeier, F., 1992. Long-term monitoring of biological diversity in tropical forest areas: methods for establishment and inventory of permanent plots. MAB Digest 11, UNESCO, Paris, France.
- Duke, N.C., 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. *Wetlands Ecology and Management* 9, 257–269.
- Elzinga, C.L., Salzer, D.W., Willoughby, J.W., Gibbs, J.P., 2001. *Monitoring Plant and Animal Populations*. Blackwell Science, Inc., Malden, Massachusetts, USA, 360 pp.
- Ernst, K.A., Brooks, J.R., 2003. Prolonged flooding decreased stem density, tree size and shifted composition towards clonal species in a central Florida hardwood swamp. *Forest Ecology and Management* 173, 261–279.
- Ewel, K.C., Twilley, R.R., Ong, J.E., 1998. Different kinds of mangrove forests provide different goods and services. *Global Ecology and Biogeography Letters* 7, 83–94.
- Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J.I., Cadamuro, L., 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia* 115, 39–53.
- Gong, W.K., Ong, J.E., 1995. The use of demographic studies in mangrove silviculture. *Hydrobiologia* 295, 255–261.
- Holdridge, L., Grenke, W.C., Hatheway, W.H., Liang, T., Tosi, J.A., 1971. *Forest Environment in Tropical Life Zones*. Pergamon Press, NY, 747 pp.
- Holmgren, P., Thuresson, T., 1998. Satellite remote sensing for forestry planning—a review. *Scandinavian Journal of Forest Research* 13, 90–110.
- Holmgren, P., Thuresson, T., Holm, S., 1997. Estimating forest characteristics in scanned aerial photographs with respect to requirements for economic forest management planning. *Scandinavian Journal of Forest Research* 12, 189–199.
- Imbert, D., Ménard, S., 1997. Structure de la végétation et production primaire dans la mangrove de la Baie de Fort-de-France, Martinique (F.W.I.). *Biotropica* 29 (4), 413–426.
- Imbert, D., Labbé, P., Rousteau, A., 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. *Journal of Tropical Ecology* 12, 663–680.
- Imbert, D., Rousteau, A., Labbé, P., 1998. Ouragans et diversité biologique dans les forêts tropicales. L'exemple de la Guadeloupe. *Acta Oecologica* 19 (3), 251–262.
- Jayatissa, L.P., Dahdouh-Guebas, F., Koedam, N., 2002. A review of the floral composition and distribution of mangroves in Sri Lanka. *Botanical Journal of the Linnean Society* 138, 29–43.
- Kairo, J.G., 2001. *Ecology and restoration of mangrove systems in Kenya*. PhD dissertation, Vrije Universiteit Brussel, Brussels, Belgium, 110 pp.
- Kairo, J.G., Kiviyatu, B., Koedam, N., 2002a. Application of remote sensing and GIS in the management of mangrove forests within and adjacent to Kiunga Marine Protected Area, Lamu, Kenya. *Environment, Development and Sustainability* 4 (2), 153–166.
- Kairo, J.G., Dahdouh-Guebas, F., Gwada, P.O., Ochieng, C., Koedam, N., 2002b. Regeneration status of mangrove forests in Mida Creek, Kenya: a compromised or secured future? *Ambio* 31 (7/8), 562–568.
- Kent, M., Coker, P., 1992. *Vegetation Description and Analysis. A practical Approach*. John Wiley & Sons, Chichester, UK, 361 pp.
- Komiyama, A., Havanond, S., Srisawatt, W., Mochida, Y., Fujimoto, K., Ohnishi, T., Ishihara, S., Miyagi, T., 2000. Top/root biomass ratio of a secondary mangrove (*Ceriops tagal* (Perr. C.B. Rob.) forest. *Forest Ecology and Management* 139, 127–134.
- Kovacs, J.M., 1999. Assessing mangrove use at the local scale. *Landscape and Urban Planning* 43, 207–208.
- Krauss, K.W., Doyle, T.W., Twilley, R.R., Smith III, T.J., Whelan, K.R.T., Sullivan, J.K., 2005. Woody debris in the mangrove forests of South Florida. *Biotropica* 37 (1), 9–15.
- Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601–615.
- Lugo, A.E., 1997. Old-growth mangrove forests in the United States. *Conservation Biology* 11 (1), 11–20.
- Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. *Annual Review of Ecology and Systematics* 5, 39–64.
- Martin, G.J., 2004. *Ethnobotany: A Methods Manual*. Earthscan Publications Ltd., London, UK, 268 pp.
- Montès, N., Gauquelin, T., Badrib, W., Bertaudière, V., Zaoui, El.H., 2000. A non-destructive method for estimating above-ground forest biomass in threatened woodlands. *Forest Ecology and Management* 130, 37–46.
- Mueller-Dombois, M., 1968. Ecogeographic analysis of a climate map of Ceylon with particular reference to vegetation. *The Ceylon Forester* 8 (3/4), 1–20.
- Nissen, T.M., Midmore, D.J., 2002. Stand basal area as an index of tree competitiveness in timber intercropping. *Agroforestry Systems* 54 (1), 51–60.
- Ong, J.E., Gong, W.K., Wong, C.H., 2004. Allometry and partitioning of the mangrove, *Rhizophora apiculata*. *Forest Ecology and Management* 188, 395–408.
- Putz, F.E., Chan, H.T., 1986. Tree growth, dynamics, and productivity in a mature mangrove forest in Malaysia. *Forest Ecology and Management* 17, 211–230.
- Saenger, P., 2002. *Mangrove Ecology, Silviculture and Conservation*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 360 pp.
- Slim, F.J., Gwada, P.M., Kodjo, M., Hemminga, M.A., 1996. Biomass and litterfall of *Ceriops tagal* and *Rhizophora mucronata* in the mangrove forest of Gazi Bay, Kenya. *Marine and Freshwater Research* 47, 999–1007.
- Smith III, T.J., 1992. Forest structure. In: Robertson, A.I., Alongi, D.M. (Eds.), *Tropical Mangrove, Ecosystems*, Washington D.C., USA, pp. 101–136.
- Stieglitz, T., Ridd, P.V., 2001. Trapping of mangrove propagules due to density-driven secondary circulation in the Normanby River estuary, NE Australia. *Marine Ecology Progress Series* 211, 131–142.
- Suzuki, E., Tagawa, H., 1983. Biomass of a mangrove forest and a sedge marsh on Ishigaki Island, South Japan. *Japanese Journal of Ecology* 33, 231–234.
- Tam, N.F.Y., Wong, Y.S., Lan, C.Y., Chen, G.Z., 1995. Community structure and standing crop biomass of a mangrove forest in Futian Nature Reserve, Shenzhen, China. *Hydrobiologia* 295, 193–201.
- Tomlinson, P.B., 1986. *The Botany of Mangroves*. Cambridge University Press, Cambridge, UK, 419 pp.
- Verheyden, A., 1997. Ruimtelijke analyse van flora en fauna in mangrovegebieden van Sri Lanka. Luchtfoto-interpretatie en GIS toepassing in het onderzoek naar mangrovedynamiek. MSc. Biology Thesis, Vrije Universiteit Brussel, Brussels, Belgium, 153 pp.
- Verheyden, A., Dahdouh-Guebas, F., Thomaes, K., De Genst, W., Hettiarachchi, S., Koedam, N., 2002. High resolution vegetation data for mangrove research as obtained from aerial photography. *Environment, Development and Sustainability* 4 (2), 113–133.
- Walters, B.B., 2005. Patterns of local wood use and cutting of Philippine mangrove forests. *Economic Botany* 59 (1), 66–76.
- Woodroffe, C.D., 1985. *Studies of a mangrove basin, Tuff Crater, New Zealand: I. Mangrove biomass and production of detritus*. *Estuarine, Coastal and Shelf Science* 20, 265–280.



000116190 500500 0602