ARTICLE

An individual-based model of long-term forest growth and carbon sequestration in planted mangroves under salinity and inundation stresses

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Abstract—We developed a spatially explicit individual-based model of forest development trajectories of monospecific *Rhizophora mucronata* plantations. The model incorporates stochastic initial seedling spacing, propagule dispersal, recruitment, and mortality. We simulated and compared the growth, development and accumulation of carbon stocks of restored mangroves between optimal and sub-optimal settings. Salinity is considered as a stressor, while flooding effects are described as an inundation stress factor. In the optimal setting, the simulated mangrove population accumulated large aboveground carbon stocks (of around 140 T/ha) after 100 years. Under sub-optimal conditions, we observed delayed maturity by at least 10 years near the salinity threshold and the carbon stock decreased through time towards much lower values (25 T/ha). More importantly, the continuous presence of stressors may lead to forest population collapse (at 50 yrs post-planting) probably as a result of the accumulated effects of physiological stresses. Thus, restored mangrove populations that are located in highly saline and frequently inundated sites, may eventually collapse even though they may appear to be healthy in the early stages of forest development. Our results imply that current and future restoration practices should carefully consider site selection in order to ensure viable long-term forest development and to have an optimum contribution to carbon sequestration.

Keywords—mangroves, individual-based model, growth, forest development, restoration trajectory, salinity, inundation, carbon sequestration

INTRODUCTION

Mangrove restoration programs have long been implemented in the Philippines (Walters 2003) receiving funding from the local government, national government, non-government organizations and international funding agencies. Mangrove restoration has recently been considered as a climate change adaptation and mitigation strategy because of its potential role in the sequestration of atmospheric CO₂ (Donato et al. 2011). The effectiveness of a mangrove restoration program, however, depends on the growth and survival of the planted mangroves and, subsequently, the long-term stability of the forest.

In the Philippines, most mangrove plantations are located in sub-optimal settings that are highly saline and frequently inundated (Samson and Rollon 2008). The coastal fringe is considered sub-optimal for mangrove planting. Most restoration programs commonly use *Rhizophora spp*. due to their relative ease of sourcing and transplanting propagules as compared to the more appropriate *Sonneratia* or *Avicennia spp*. But *Rhizophora mucronata*, in particular, is known to be stenohaline and thus disadvantaged in areas where tidal frequencies (hence, salinity fluctuations) are high. Waves further make the coastal fringes less suitable for *R. mucronata* as wave action will erode the substrate and reduce the stability of the planted seedlings. Most mangrove planting programs are implemented in

*Corresponding Author Email Address: ssalmo@ateneo.edu Submitted: May 18, 2015 Accepted: June 16, 2015 Published: July 28, 2015 numerous sites deemed biophysically unsuitable for *R. mucronata*. Primavera and Esteban (2008) cite policy-related reasons for the persistence of such restoration malpractice. Most of the planted seedlings have stunted growth and poor survival. However, monitoring the growth and survival as well as the success or failure of these mangrove restoration programs is largely not undertaken. If any monitoring is conducted, the findings are rarely reported.

Due to the long periods of time needed for the growth and development of mangrove forests, assessment of the success of mangrove restoration programs is challenging. Mathematical models offer a way to circumvent this challenge. However, available mangrove forest models such as KiWi (Berger and Hildenbrandt, 2000) and FORMAN (Chen and Twilley 1998) have built-in assumptions regarding environmental conditions that are more applicable for subtropical mangrove systems (Berger et al. 2008). In their original configuration, these existing models are not ideal for mangrove systems in the Philippines, which thrive under remarkably different environmental conditions. On the other hand, the MANGRO model (Doyle and Girod, 1997) is more applicable to the Philippine setting because it considers the effect of tidal flooding on tree growth. However, it does not provide a mechanism for seedling or sapling dispersal (Berger et al. 2008)

Here, we used model simulations to compare the long-term trajectories of forest development and carbon stock accumulation between settings that mimic typical reforested sites in the Philippines and those considered biophysically optimal for $R.\ mucronata$. The model we developed for this study combines the

strengths of KiWi in describing resource competition and salinity sensing, and of MANGRO in considering tidal inundation as a stressor that attenuates the growth rate and survival of individual mangroves. In addition, our model incorporates stochastic recruitment, dispersal, and mortality, which are not considered simultaneously in any of the said models. We do not account for wave exposure in this study by assuming that extreme wave action does not occur frequently. The biophysical parameters of planted *R. mucronata* required to specify the model inputs are deduced by fitting simulation results with actual growth monitoring data obtained from our recent field observations (Salmo III et al. 2013). We tracked the development trajectories of virtual mangrove forests over a period equivalent to 100 years, although the model could be simulated over longer periods of time.

MATERIALS AND METHODS

Model development

The model is a spatially explicit, individual-based model founded upon a description of the rate of change of the diameter-at-breast-height, *dbh*. The *dbh* is used as a gauge for the growth of individual mangroves. Allometric relations can estimate the growth rate of other aspects of mangrove structure (i. e., crown diameter) and biomass by extrapolating *dbh* (Botkin 1972). In the model, growth stressors are represented by a salinity stress factor and inundation stress factor where the value 1 indicates the absence of the stressor (hence, optimal condition). Competition between individual mangroves is computed based on the Field of Neighborhood (FON) approach and the Zone of Influence (ZOI) concept in the KiWi model (Berger and Hildenbrandt 2000). In the presence of stressors and resource competition, the growth of an individual mangrove is given in Equation 1 (for convenience, *dbh* is renamed as *D*), as:

$$\frac{dD}{dt} = \left(\frac{\Omega}{2+\alpha}\right)D^{\beta-\alpha-1} \left[1 - \frac{1}{\gamma} \left(\frac{D}{D_{max}}\right)^{1+\alpha}\right] * C * S * E \tag{1}$$

where $\alpha=0.95$ and $\beta=2$ are allometric constants for height and tree crown, respectively, as a power function of D. The constant Ω , is a conversion factor with a value of 0.25 to harmonize the left and right sides of Equation 1. The values for α and Ω were derived from the growth and biomass of planted mangroves as reported in Salmo III et al. (2013) while β was derived from the allometric relation of D and leaf area index (LAI; Botkin 1972). Thus, the simulation of a given time scale (i.e. day, month, year) can be changed without necessarily losing its generality. Meanwhile, γ and D_{max} are set based on the maximum possible height $H_{\text{max}}=130$ m (Koch et al. 2004). Because an individual mangrove is confronted by resource competition in a forest, the growth rate is slower on average within a forest or within patches of trees than in isolation. Lastly, the factor C represents the attenuation to the growth rate of an individual mangrove caused by competition with other mangroves. Competition is further explained in a later section.

The stress factors S and E due to salinity and inundation, respectively, are valued between 0 and 1. Coastal fringe conditions are represented by 0, whereas mid-intertidal conditions by 1. Based on Equation 1, a value close to zero would decrease growth with time such that the individual mangrove grows at a slower pace. In particular, E attenuates the average growth rate because of stress caused by submergence (partially or totally) under waterlogged condition. The diurnal cycles of the tides also cause fluctuations in salinity levels. Although tidal flooding and salinity appear correlated, we assume in our model that these factors are separable. While this assumption adds tractability, it is nevertheless a limitation of the model. In our model, we set the mangroves to grow optimally if salinity is ≤ 25 ppt and will be stressed if salinity will be 27 ppt (S = 0.38), 29 ppt (S = 0.27) and 40 ppt (S = 0.02). The associated values of S are determined from salinity x by a sigmoidal response function: $S = S(x) = \{1 + \exp[0.25(x - 25)]\}^{-1}$. Similarly, growth of mangroves will be optimal if they are not inundated (E = 1; representing mean tidal level) but will be constrained if they are inundated for 4-6 hours (E = 0.90), 6-8 hours (E = 0.75) and 8-12 hours (E = 0.50) per 24-hr cycle (Table 1).

TABLE 1. Growth factors due to *R. mucronata* for salinity (regulator) and inundation (hydroperiod) in optimal and sub-optimal settings.

Factor	Description	Optimal value	Sub-optimal values
S	Salinity stress factor	1.0	0.38, 0.27, 0.10, 0.05, 0.02
Ε	Inundation stress factor	1.0	0.90, 0.75, 0.50

We explored the long-term growth, development, and carbon stock accumulation of restored R. mucronata forests by comparing different salinity and inundation settings. Each setting is mathematically represented as an ordered pair (S, E) of the two factors listed in Table 1. The software implementation of the model was made using the C++ programming language on a Unix platform in a 1.7 GHz Intel Core i5 machine. A detailed description of a related model using the "Overview-Design-Detail" (ODD) framework is provided in Juanico and Salmo III (2014).

Initialization

A $40\text{m} \times 40\text{m}$ (= 0.16 ha) mangrove patch is initialized. The simulation moves forward with an annual time step ($\Delta t = 1$ year). In the beginning, there are 100 seedlings of R. mucronata with initial dbh of 0.5 cm that are scattered somewhat randomly at 1.0-1.5 m distance apart. Thus, the distance of one seedling to another is about 1.0-1.5 m, which approximates the typical planting

density for most mangrove restoration sites in the Philippines (Samson and Rollon, 2008)

The simulated mangrove forest was assumed to have uniform, unchanging salinity level. We also assumed that the tidal exposure of the forest leads to a uniform, unchanging inundation stress. Here, we consider inundation stress as a time-averaged effect of tidal exposure over a long period of time. Note that inundation stress does not denote tidal cycle. Since the mangrove plantation is monospecific, then all parameters listed in Table 1 were fixed at the beginning of a simulation. The simulations were run for five times for each S and E setting.

Growth

Equation 1 was numerically solved for each mangrove in the patch. Using $\Delta t = 1$, the solution was implemented using Euler's forward scheme. Consequently, the dbh of an individual mangrove was increased by an amount approximately equal to the right-hand side of Equation 1 at time t. The life stage of the mangrove was determined by means of the following standard classification based on dbh: seedling, $0.50 \le dbh < 2.50$ cm; sapling, $2.50 \le dbh < 5.0$ cm; and tree, $dbh \ge 5.0$ cm. By implementing a positivity constraint on Equation 1, the value of dbh was only expected to increase as time progresses.

Recruitment

Based on our field data (Salmo III et al. 2013), an annual average of five seedlings from each mature R. mucronata tree was recruited. Established seedlings have initial dbh of 0.50 cm, and were scattered randomly within a 5 m radius around the parent tree. The recruitment by each mature mangrove was also taken as a stochastic process with a constant probability per unit time. Therefore, the total number of recruits at any given time was a random variable. This randomness reasonably accounted for the probabilistic survival of recruits due to many other confounding factors, e.g., predation, disease, or wave-current action, which were not explicitly accounted for in the present model.

Mortality

The loss of individuals due to mortality was described as a stochastic process with a probability of death that approximated the total mortality rate of the entire population. Due to confounding factors, such as predation or pest infestation, each individual mangrove has a constant chance of dying at any given point in time. The rate of mortality becomes higher as tree density increased due to more intense resource competition or as the available growing spaces are occupied (cf. Oliver and Larsson 1996).

Mangrove mortality rates are expected to conform with Type III survivorship curves, as any plant in general (Schaal and Leverich 1982). The life stage (e.g., seedling, sapling or tree) determines the mortality rate. Seedlings have the highest mortality rates, whereas trees have the lowest. Dying in the population is treated as a Poisson process. Any mangrove has a chance of dying at any given point in time. The probability of dying within a certain time period of a mangrove at a given life stage is related to its mortality rate. Because progression through life stages by growth is constrained by resource competition, the probability of dying is indirectly related to population density.

Competition

We modeled tree-to-tree competition following the approach in the KiWi model. One of the strengths of the KiWi model is its generic approach in describing resource competition in a forest. We followed closely the FON approach for calculating the intensity of competition based on the dbh size and the position of an individual mangrove in the forest (Berger and Hildenbrandt 2000). In this method, an individual mangrove is affected by competition with its neighbors. The effect on the individual is a slowdown to its growth. Neighbors at a distance contribute to this effect through an extended root system below the ground and a tree crown aboveground. The aggregate effect on an individual from all other mangroves is best described mathematically using field variables. If the aggregate field on a mangrove at position (x,y) is F, then the attenuation factor it contributes toward the slowdown of the growth rate is C(x,y) given below:

$$C(x,y) = 1 - 2F(x,y)$$
 (2)

Carbon stock

Biomass evidently increases as the mangrove grows. Because the model tracks growth by observing the dbh, we used an allometric equation (cf. Komiyama et al. 2008) to convert a mangrove's dbh to above-ground biomass (AGB, in kg per tree):

$$AGB = 0.235 \times dbh \tag{3}$$

Dispersal

A propagule from a tree may establish and grow anywhere within an annular region surrounding the tree. This annular region has an inner radius equal to the parent tree's crown radius. On the other hand, its outer radius is equal to the product between time and dispersal rate. The dispersal rate is species-specific. For *R. mucronata*, we assume that this rate is about 26.67 cm per day deduced from measurements by Sousa et al. (2007). Stochasticity was incorporated by assigning a random position with respect to the vertical axis of the parent tree. The stochastic dispersal addresses the uncertainty in tracking the exact site where a seedling establishes.

RESULTS

Spatial distribution

The snapshots of mangrove forest growth and development under the optimal setting, (S, E) = (1, 1) for t at 5, 25, 50, and 100 years are shown in Figure 1. The perimeter enclosing all mangroves is called the convex hull where all mangrove individuals (seedlings, saplings and mature trees) per simulation are confined. The values for tree density, aboveground biomass, and carbon stocks were computed based on the set area of the mangrove patch. The use of the convex hull, rather than the entire patch, shows a more accurate description of the actual spatial distribution of mangroves. The density of mature trees increased with time. As time progressed, there was an apparent increase in the number of mature trees accompanied by the decrease in available growth spaces as a result of tree-to-tree competition. The fact that the tree density is increasing at the optimal setting (1,1) implied that AGB also increased as time progressed.

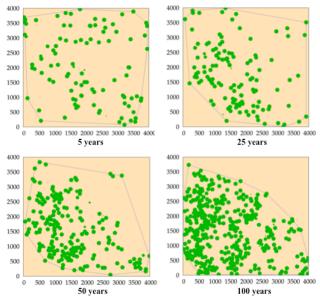


Figure 1. Development of restored mangrove forest over 100 years for the optimal setting (S=1, E=1). The zero (0) point in the Y-axis denotes the edge of the shoreline. Each graph represents a snapshot of mangrove distribution 5, 25, 50, and 100 years post-planting. Each dot represents the top view of the crown (computed from dbh) of an individual mangrove. The indicated perimeter is the convex hull, which encloses the area occupied by all mangrove individuals.

Long-term carbon stock accumulation

Based on the different possible ordered pairs (S,E) of values listed in Table 1, the time-averaged levels of aboveground carbon stock at 100 years increased with time [n= five replicates of each (S,E)]. Figure 2 depicts the long-term mean carbon stock of the forest under different settings provided in Table 1 $(S=\{0.02,0.5,0.10,0.27,0.38,1.00\}$ and $E=\{0.50,0.75,0.90$ and $1.00\}$. The average aboveground carbon stock at 100 years for the optimal setting (1,1) is about 140 tC/ha. Compared to the sub-optimal settings, the optimal result was found to be considerably higher by at least 60 tC/ha. Generally, for any value of S considered, the trend for carbon stock with respect to E was positive except for S=0.38. On the other hand, the long-term carbon stock significantly declined when S was less than 0.1, to levels at least an order of magnitude lower than the optimal value (Figure 2).

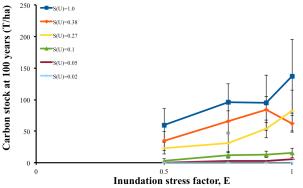


Figure 2. Long-term carbon stock accumulated after 100 years for different (S, E) settings. Each data point represents the average of five simulations for a given setting. The error bars indicate the standard deviation from the mean. The deviation from the expected monotonic trend for (0.27, 1) and (0.38, 1) can be explained in part by the salinity response S(x). The sigmoidal graph of S(x) puts the salinity levels associated with S=0.27 and S=0.38 at the transition part. The transition is associated with more statistical uncertainty.

There was a pronounced difference in the carbon stock trajectories between the optimal setting and the most extreme sub-optimal setting. Simulations showed a continuous accumulation of carbon stock due to increasing tree density for up to 100 years since initial planting for the optimal setting (Figure 3). In contrast, in the most extreme sub-optimal setting (S=0.02;E=0.05), seedling density decreased rapidly within the first 10 years, then the remnant population (composed of surviving saplings that eventually matured as trees) finally collapsed around 50 years (Figure 4B). Consequently, the carbon stock in living mangroves was non-existent after 50 years (Figure 4A). For sub-optimal settings, S and E are smaller than unity, so that plants would linger in the less mature state for a longer time (see Equation 1). Since immature trees are more susceptible to mortality than mature trees, then other instantiations of the sub-optimal settings are likely to lead to decreases in populations and carbon stock over time.

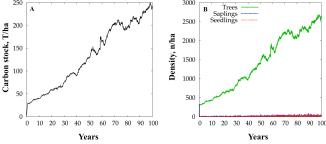


Figure 3. Trajectory of (A) carbon stock, and (B) density of trees, saplings and seedlings over 100 years in a single realization of the model for the optimal setting (S=1, E=1).

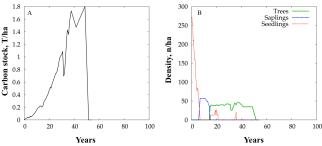


Figure 4. Trajectory of (A) carbon stock, and (B) density of trees, saplings and seedlings over 100 years in a single realization of the model for the extreme sub-optimal setting (0.02, 0.50).

Effect of salinity stress

Simulations suggested that the density of mature trees (> 0.5 cm dbh) under different values of S (with a fixed value E=1) will increase through time for S=0.27,0.38, and 1.0 (Figure 5). The forest growth rate is indicated by the slope of the trajectory, which is most positive (i.e., highest rate of increase in tree density) for the optimal case S=1. On the other hand, below an unidentified threshold (ca. 0.02 < S < 0.27), the trajectory trends downward or the slope is negative. For S=0.02, the development of mature trees occurred at a later time than for the other less stressful S values. The delay could be explained by the slow growth, and thus slow transition, of individual mangroves (from seedling to sapling then from sapling to tree) in a sub-optimal salinity setting even in the absence of inundation stress.

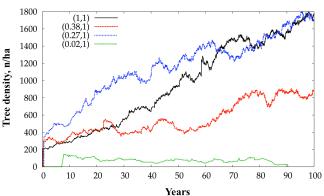


Figure 5. Trajectory of changes in tree density with time for the different values of the salinity stress factor S at the optimal value of the inundation stress factor, E = 1. Each line is a single realization of the (S, E) setting.

Effect of inundation stress

The density of mature trees (with a fixed value S=1) had an upward trajectory through time regardless of E values considered (Figure 6). The slope was highest for the optimal case (E=1), indicating fastest forest growth rate. The highest tree density 100 years post planting was achieved at the optimal value. Unexpectedly, tree density after 100 years was higher for E=0.5 as compared to E=0.75. This may have been an artifact of the simulations due to stochasticity. The

fact that tree density had a consistent upward trend regardless of *E* values considered strongly suggests that *R. mucronata* is less sensitive to wide variations to inundation stress compared to salinity stress.

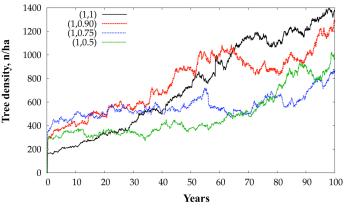


Figure 6. Trajectory of changes in tree density with time for the different values of the inundation stress factor E at the optimal value of the salinity stress factor, S = 1. Each line is a single realization of the (S, E) setting.

DISCUSSION

Individual-based model for restored monospecific mangroves

Our model provides a platform that analyzes the restoration trajectory of planted monospecific mangroves, in this case of the species *Rhizophora mucronata*. We adapted the Field of Neighborhood approach and the concept of Zone of Influence from the KiWi model (Berger and Hildenbrandt 2000). However, we incorporated several improvements based on actual *R. mucronata* plantation data in the Philippines (Salmo III et al. 2013) and adjusted other model assumptions to approximate Philippine environmental conditions. Hence, our model can be used to project the possible development or demise of typical mangrove restoration programs in the Philippines.

We evaluated the effects of different levels of salinity and inundation in the model. These parameters are the main stressors that can strongly constrain the growth and survival of planted mangroves (see Samson and Rollon 2008 for example). The growth of mangroves, particularly of the species *R. mucronata*, is physiologically sensitive to high salinity (>25 ppt) and prolonged periods of inundation (>4 hours submergence per 24-hour cycle). The salinity and inundation settings that we used in the model were derived from long-term field observations (10 years or more) at various mangrove restoration sites across the Philippines (Salmo III et al. 2013). In our simulations, we evaluated the effects of salinity levels that were not higher than 40 ppt. Note, however, that most replanted sites can have extreme salinity levels of up to 60 ppt, which will have stronger adverse effects on mangrove growth and survival.

We also modified the mechanism of propagule dispersal, mortality and stochasticity from the KiWi model. The propagules are transported and able to successfully establish only within a 5 m radius from the parent tree. This limited range of dispersal is consistent with observations in the field. This is probably due to the limited buoyancy of the propagules as well as the fact that propagules can often be stranded in the dense network of prop roots of *R. mucronata*. Mortality in the model is probabilistic. The probability of dying is negatively associated with age and positively associated with the rate of increase in the diameter of an individual tree, hence mortality rate is higher for seedlings and lower for mature trees. In terms of stochasticity, we did not define the time to which an individual mangrove can transition from seedling to sapling or from sapling to tree, but instead let the change in *dbh* determine its life stage.

Our modifications of the KiWi model are consistent with our field observations. However, we acknowledge some possible limitations of our model. Factors such as spatial gradients in salinity and inundation levels as well as the strength and direction of water currents in the entire patch relative to distance from the shoreline will obviously have an effect on the growth and survival of each individual mangrove. These limitations are currently being addressed in an ongoing complementary study. Nonetheless, we believe that the present model was able to capture the general pattern of growth of individual mangrove and critical parameters in the dynamics of mangrove populations. This would then enable the simulation and assessment of long-term restoration trajectories of planted mangroves.

Optimal vs. sub-optimal conditions

As expected, the restoration trajectories (in terms of changes in tree density, aboveground biomass and carbon stock with time) of mangroves varied widely between optimal and sub-optimal settings (Figures 2, 4, 5 and 6). Under optimal conditions, the mature trees (> 5 cm dbh) appeared to be sporadically distributed at the 5th and 25th yr but tend to be more congregated on the 50th and 100th yr (Figure 1). Such a distribution pattern was probably due to the limited range of propagule dispersal (only 5 m from the parent tree) that we imposed for R. mucronata in the model. These results are also consistent with our field observations. However, they contrast with the results of simulations by Berger and Hildenbrandt (2000) for R. mangle, a neotropical mangrove species. In their study, the trees were almost uniformly distributed until the available growing spaces (cf. Oliver and Larsson

1996) were occupied. Such contrasting results between the two studies can be attributed to the effect of inundation (which was not explicitly accounted for by Berger and Hildenbrandt 2000) as well as the combined effects of salinity and inundation. The presence of these stressors will most likely result in better establishment and growth of individual trees in areas closer to the shoreline.

The trajectories suggest that the density of mature trees rapidly increases within a very short time (<10 years) to about 150-400 trees/ha in all scenarios, except when S=0.2, E=1 (Figures 5 and 6). Furthermore, the increase was apparently the steepest for the optimal setting, S=1, E=1, between the 10^{th} and 70^{th} years. Compared to the baseline, the increase in the trend for sub-optimal settings is relatively flatter in the said period.

The simulated aboveground biomass and carbon stocks here are remarkably lower compared to published reports (see Donato et al. 2012 for example). However, the low carbon stock values are similar to those reported for Philippine mangrove plantations (55 – 60 tC/ha; Salmo III et al. 2013). Even in the optimal settings (S=1,E=1), the biomass and carbon stocks are also low (between 71 and 209 tC/ha at 100 years in the simulations) which can probably be accounted for by the low diversity of the restored system (see also Isbell et al. 2013). Also, the model implies that to have optimum growth, *Rhizophora* seedlings must be planted above the mean tidal level.

A striking result of our simulations is the sudden collapse of the mangrove population (and subsequently carbon stock) at 50 years post planting particularly under the most extreme sub-optimal conditions (Figure 4). Such a population collapse, while still largely undocumented for current mangrove restoration sites in the Philippines, makes sense ecologically because of the persistent presence of physiological stressors that could eventually lead to the demise of the planted mangroves. A monospecific plantation is known to be less resilient against stressors as compared to a more diverse mangrove forest system (Gunderson 2000). Thus, while we acknowledge that mangrove restoration programs can contribute to carbon sequestration, the amount and rates of carbon sequestered by typical mangrove restoration efforts are likely to be very low and there is a possibility that the planted mangroves may perish in the long run.

Management implications

Mangrove restoration has long been practiced in the Philippines (see Talaue-McManus et al. 1999; Walters 2003; Salmo et al. 2007; Primavera and Esteban 2008; among others). However, very few successful cases have been reported. Many programs have failed basically because of inappropriate species-substrate matching and planting in unsuitable locations (Samson and Rollon 2008). These monospecific restoration programs have long been criticized due to the stunted growth and poor survival of mangroves and their potential effect of reducing mangrove species diversity (Primavera and Esteban 2008).

The use of mangrove restoration programs to mitigate the impacts of global warming seems like a viable strategy and provides additional incentives for mangrove managers. Planted mangroves can of course contribute to the sequestration of atmospheric CO₂. However, restored mangroves will be effective in carbon sequestration over the long term only if the mangrove population will have steady growth and maintain its stability. Unfortunately, this is not the case yet for most mangrove plantations in the Philippines.

In our simulation results, we demonstrated that mangroves (Rhizophora sp.) planted in sub-optimal conditions would have much lower levels (up to 100%) of aboveground biomass and carbon stock 100 years post-planting compared to those planted in optimal conditions due to mortality. In addition, the population collapse that may occur around 50 years post-planting implies the need for frequent replanting at the same site in order to maintain the population. Thus, although the planted mangroves may initially appear to be healthy (for example even at 20 years post-planting), there is a possibility that the population will collapse in the long run because of the persistence of stressors and the cumulative effects of physiological stresses. Therefore, the accumulated carbon stocks in the restored mangrove systems planted in sub-optimal conditions may be in danger of being lost over time. Hence, we emphasize the importance of the appropriateness of the planting site in terms of the levels of salinity and inundation stresses. There are other factors that have not been considered explicitly, such as wave stress. However, in the model we presented here, we focused on evaluating the impacts of extreme salinity and inundation stress levels in the backdrop of tree competition and seed dispersal. Despite its limitations, the model offered some important insights about long-term forest growth and carbon sequestration. We considered the presence of stressor gradients in a separate study (see Juanico and Salmo III 2014).

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CONFLICTS OF INTEREST

None

CONTRIBUTION OF INDIVIDUAL AUTHORS

Dr. Salmo conceptualized and implemented the study. Dr. Salmo wrote the introduction and discussion sections. Dr. Juanico developed the model and analyzed the results of simulations. Dr. Juanico also wrote the methods and results sections.

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