MODELLING NATURAL MORTALITY OF TROPICAL PLANTATION SPECIES Acacia mangium Willd.

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ABSTRACT

Natural mortality of trees is extremely variable due to the uncertainty and complexity of the functioning of forest ecosystems. To overcome this uncertainty, a two-step mortality model was applied for unthined stands of *Acacia mangium* species. The model was developed using data from 197 permanent sample plots measured periodically at 1-yr time intervals from 2-4 yrs until 8-11 yrs after planting in South Sumatra, Indonesia. The model consists of two complementary equations. The first equation is a logistic function predicting the probability of mortality incidence depending on stand density, site index and stand age. The second equation estimates the reduction in the number of surviving stems observed in a stand where natural mortality occurs. Nine equations were fitted using data from permanent sample plots where trees died over the time period and the best model was selected. Estimates from this second model are then adjusted by a factor equal to the probability of mortality applying three different approaches: probabilistic two-step, deterministic threshold and stochastic. All methods reveal no significant difference between the observed and the predicted number of surviving stems per ha. The probabilistic two-step approach, however, produces more consistent and the most accurate estimates. This method should provide reliable prediction when it is to be used in forest productivity prediction and management system for the species.

Keywords: logistic function, mangium, mortality model, stand density, survival.

INTRODUCTION

Mortality of trees is a natural process that plays important roles in forest ecosystems and has a strong impact on stand production. This information needs to be accurately estimated as forest productivity may be sensitive to periodic lost due to mortality, especially over longer period of time with changing climate (Zhang et al. 2015, Ma et al. 2016). However, natural mortality of trees is extremely variable and difficult to predict due to the uncertainty and complexity of the functioning of forest ecosystems (Monserud and Sterba 1999, Fridman & Ståhl 2001, Ma et al. 2016). Natural mortality of trees can be distinguished into two types: regular (non-catastrophic) and irregular (catastrophic) mortality. Regular mortalities, can be defined as being due to suppression and competition between trees for light, water and soil nutrients within a stand; while irregular mortality

Generally, only regular mortality is considered when modelling survival or stand density and data from sample plots showing excessive mortality caused by catastrophic events are usually excluded from analyses (Amateis *et al.* 1997, Woollons 1998, Diéguez-Aranda *et al.* 2005). Regular mortality is more predictable than irregular mortality (Murty & McMurtrie 2000), particularly at tree and stand levels, but not necessarily at a landscape level (Alenius *et al.* 2003).

In an attempt to simplify an approach to such a complex phenomenon, mortality has been commonly modelled within individual tree or stand level, either as regular or irregular mortality. Models for predicting mortality or survival have been developed, particularly for some species growing in temperate forests, such as *Pinus taeda* (Avila & Burkhart 1992, Amateis *et al.* 1997, Lee & Coble 2002), *Pinus elliottii* (Pienaar & Shiver 1981,

is caused by random disturbances or hazards such as fire, wind, landslide, pest and disease outbreaks (Vanclay 1994).

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Bailey et al. 1985, Pienaar et al. 1990), Pinus radiata (Woollons 1998, González et al. 2004), Pinus sylvestris (Diéguez-Aranda et al. 2005), and Picea glauca (Evert 1981, Yang et al. 2003). In contrast, a very few mortality models have been published for tropical plantation species (Forss et al. 1996).

In Indonesia, natural mortality of trees in a stand has usually been predicted simply as a mean annual mortality rate. Accurate prediction of natural mortality at the stand level is important, particularly for tropical species such as Acacia mangium which has been planted largely to meet the demand for wood industries. This prediction should be included in the management system to maintain the forest productivity and mitigate the risk of potential loss due to mortality. Forss et al. (1996) developed a model for predicting survival of A. mangium species in South Kalimantan, but it was based on data from only a small number of semi-permanent sample plots and covered young ages only. To provide reliable information for estimating forest productivity, a more accurate mortality model for various stand conditions and covers the longer time period needs to be developed.

This study aimed to develop a stand level mortality model for *Acacia mangium*, one of the most commonly tropical species planted in Indonesia (FAO 2002, Krisnawati *et al* 2011, Krisnawati 2016), by relating mortality to stand variables that affect the natural mortality process. Different causes of mortality are not separated so the model combines regular mortality due to suppression or normal competition and irregular mortality from random disturbances.

MATERIALS AND METHODS

Data Description

Data for this study were based on measurement of 197 permanent sample plots established subjectively in *A. mangium* unthinned stands in South Sumatra, Indonesia. The study area has a lowland humid environment which well suited for growing *A. mangium*. The plots are good representative for the study site representing the range of ages, stand densities and site qualities. All plots were 0.1 ha in size but their initial planting spacing varied. Almost all of the plots were remeasured at 1-yr time intervals until 8-11 yrs of

age. For each measurement, the following stand variables were calculated: stand density in terms of total number of stems per ha (N), basal area per ha (B), dominant height (H), site index (S) which follows a function of Krisnawati *et al.* (2009), and relative spacing index (RS) which is a function of the number of stems per ha and the mean dominant height (Husch *et al.* 2003). Summary statistics including mean, minimum (min), maximum (max) and standard deviation (SD) of these variables for the initial measurement of each period are presented (Table 1). The data were split randomly into two set: 75% was used for model fitting and 25% was used for model validation.

Proportion of dead stems in the plots was recorded during the re-measurement times. Natural mortality (at least one stem dying in a plot) occurred in 75.1% of the measurement periods of the fitting plots and 72.8% for the validation plots. For a few plots having measurement periods of 2 yrs, data were transformed into 1-yr using linear interpolation. The overall annual mortality rates of all available plots ranged from 0.4 to 38.3% with a mean value of 5.7%. High mortality occurred mainly in plots with very high stand densities, consistent with its resulting from extreme inter-tree competition.

Modelling Mortality

A stand level difference equation was used as the base model for modelling mortality to predict stand density at a specified projection age:

$$N2 = fN1, A2, A1() \tag{1}$$

where N_2 is number of surviving stems per ha at age A_2 , N_1 is number of surviving stems per ha at age A_1 , and the difference between A_1 and A_2 is the projection interval.

This type of equation has been commonly used for projecting stand density because of its desirable properties, including consistency, pathinvariance and the asymptotic limit of stand density approaching zero when the projected stand age (A_2) becomes very large (Clutter *et al.* 1983). However, Woollons (1998) argued that a conflict exists between the mathematical characteristics of the difference equations for stand density projection and the data used to estimate their parameters. As the most common data used for estimating mortality models are

·	Fitting data				Validation data			
Stand variable	Mean	Min	Max	SD	Mean	Min	Max	SD
Stand age (yrs)	5.5	2.0	10.0	1.8	5.2	2.0	9.0	1.7
Dominant height (m)	16.2	3.6	27.0	4.7	15.1	5.0	25.5	4.3
Site index (m)	17.8	8.4	23.9	2.7	17.1	11.7	22.8	2.3
Stand density (stems ha-1)	966	390	2020	282	882	390	1930	290
Basal area (m² ha-1)	15.7	0.7	31.6	7.2	15.2	1.8	30.4	7.4
Relative spacing index	19.0	11.1	69.5	7.5	25.8	11.8	76.2	11.1

Table.1. Summary statistics of the main stand variables at the initial measurement of each period

from repeated measurements of permanent plots, in some plots mortality may not occur, even over periods of several years (Monserud & Sterba 1999, Eid & Tuhus 2001, Fridman & Ståhl 2001). For example, in this study no mortality occurred between two successive measurements in 25.5% of the available time intervals in the full data set. If data from all plots, i.e. those in which mortality had not occurred as well as those in which it had occurred in that time interval, were included in model development, certain problems related to the binomial nature of mortality and fitting of the above model are likely to appear (Woollons 1998, Eid & Øyen 2003). On the other hand, if only data from those plots where mortality had occurred were used in model development, mortality would be overestimated.

To overcome these problems, this study followed Woollons (1998) suggestion by applying a two-step modelling approach similar to the decision theory or a probabilistic two-step approach (Hamilton & Brickell 1983) for estimating the defective volume of timber in a stand. In the first step, a model is fitted using all sample plots to predict the probability of a plot experiencing any mortality. In the second step, a model to estimate the number of surviving stems (stand density) is fitted only to the sample plots in which some mortality has occurred. Finally, the estimates derived from the second step are adjusted by a factor equal to the probability of mortality estimated in the first step to produce the overall prediction of the number of surviving stems per ha.

Predicting probability of mortality incidence

The first step in modelling mortality was estimating the probability of mortality incidence in a plot (at least one stem dying in a plot) over a 1-yr period. Incidence of mortality is considered as a discrete event with only two possible values, i.e. 0

(absence of mortality) or 1 (presence of mortality). The logistic regression model (Hosmer *et al.* 2013, Chutinantakul *et al.* 2014) was applied to predict the probability of mortality incidence:

$$\pi(x) = \frac{e^{bX}}{1 + e^{bX}} + \varepsilon \tag{2}$$

where $\pi(x)$ is the probability of mortality incidence in a plot over a 1-yr period (and the probability of no mortality is $1-\pi(x)$), x is the vector of explanatory variables which characterise the stand conditions at the initial measurement, b' is the vector of parameters to be estimated, and ε is a random error.

Due to the binary nature of dependent variable, a logit transformation is needed to estimate the parameters:

$$\hat{\pi}(x) = \frac{1}{1 + \exp(-(\hat{b}_0 + \hat{b}_1 X_1 + \dots + \hat{b}_n X_n))}$$
(3)

The explanatory variables considered for inclusion in the logistic regression model (Eq 3) are stand attributes that potentially influence the likelihood of a stem death: (1) stand density, (2) site productivity, and (3) stand vitality. The most commonly used stand density measure is the number of stems per ha (N) (Burgman et al. 1994, Wang & Hamilton 2003, González et al. 2004), stand basal area (B) (Vanclay 1991b, Yang et al. 2003, Diéguez-Aranda et al. 2005), and relative spacing index (RS) (González et al. 2004, Zhao et al. 2006). Site productivity, usually characterised by dominant height (H) or site index (S), has also been found to influence mortality (Woollons 1998, Eid & Tuhus 2001, Yao et al. 2001, Bravo-Oviedo et al. 2006). Age (A), is considered as a reasonable measure of vitality, particularly in unthinned stands, also influences the likelihood of a stem mortality (González et al. 2004, Diéguez-Aranda et al. 2005, Zhao et al. 2006). All these variables and some combinations of them were included for analysis in this study.

The generalized estimating equation (GEE) method (Stokes et al. 2012, Hosmer et al. 2013) was employed to handle correlated data in the logistic regression analysis due to serial correlation between measurements in the same plots, which has not been addressed in some previous studies (Eid & Øyen 2003, Wang & Hamilton 2003, González et al. 2004, Diéguez-Aranda et al. 2005, Zhao et al. 2006). This method is an extension of generalised linear model (GLM), suitable for binomially distributed data with repeated measurements.

Estimating stand density

The second step in modelling mortality was to develop a model to estimate stand density for a specified projection age using data from only sample plots where mortality has occurred in that time interval. Several algebraic difference equations derived from four differential equations were tested in this study as candidate models for predicting stand density (Table 2). Comparison of the model estimates was based on graphical and

numerical analyses of residuals, following the criteria as used by Krisnawati *et al.* (2009) for modelling dominant height and site index for *A. mangium*.

Adjusting the Predicted Stand Density

Final prediction of stand density involves combining the models from the two preceding steps and adjusting the predicted survival. The predictions can be calculated by deterministic and stochastic approaches (Weber *et al.* 1986, Monserud & Sterba 1999). The most common deterministic approach is based on decision theory and called a "probabilistic two-step approach" (Hamilton & Brickell 1983, Woollons 1998), where the predicted number of surviving stems per ha (N_{add}) is determined by:

$$N_{adj2} = N_1 - \hat{\pi}(x)(N_1 - \hat{N}_2)$$
 (4)

where $\hat{\pi}p(x)$ is the probability of mortality incidence over the period estimated by the logistic model (Eq.3), N_1 is the number of surviving stems per ha at the initial age A_1 , and $\hat{N}2$ is the number of surviving stems per ha at the

Table 2. Difference-equation forms of stand mortality models tested in this study

Model	Expression	References				
Mortality rate is constant, independent of age:						
M1	$N_2 = N_1 \exp\left(c_0 \left(A_2 - A_1\right)\right)$	Clutter et al. (1983)				
Mortality rate	is proportional to a power function of age:					
M2	$N_2 = \left(N_1^{-0.5} + c_0 \left(\left(A_2 / 100 \right)^2 - \left(A_1 / 100 \right)^2 \right) \right)^{-2}$	Woollons (1998)				
M3	$N_2 = \left(N_1^{-0.5} + c_0 \left(\left(A_2 / 100\right)^{b_2} - \left(A_1 / 100\right)^{b_2} \right) \right)^{-2}$	modification of M2				
M4	$N_2 = \left(N_1^{-0.5} + c_1 S \left(\left(A_2 / 100 \right)^{b_2} - \left(A_1 / 100 \right)^{b_2} \right) \right)^{-2}$	M3 with site index				
Mortality rate is proportional to a hyperbolic function of age:						
M5	$N_2 = N_1 (A_2/A_1)^{b_2} \exp(c_0 (A_2 - A_1))$	Diéguez-Aranda et al. (2005)				
M6	$N_2 = N_1 (A_2/A_1)^{b_2} \exp(c_1 S(A_2 - A_1))$	M5 with site index				
M7	$N_2 = N_1 (A_2/A_1)^{b_2} \exp(c_0 + c_1 S(A_2 - A_1))$	Bailey et al. (1985)				
Mortality rate is proportional to an exponential function of age:						
M8	$N_2 = N_1 \exp\left(c_0 \left(b_2^{A_2} - b_2^{A_1}\right)\right)$	Laar & Akça (1997)				
M9	$N_2 = N_1 \exp\left(c_1 S\left(b_2^{A_2} - b_2^{A_1}\right)\right)$	M8 with site index				

Notes: A_1 is initial age (yr), A_2 is re-measurement age (yr), N_1 is number of surviving stems per ha at age A_1 , N_2 is number of surviving stems per ha at age A_2 , and b_1 , b_2 and b_3 are model parameters to be estimated.

prediction age A_2 predicted by the selected mortality model (Table 2).

Another deterministic approach is to use a threshold value between 0 and 1. If $\hat{\pi}p(x)$ exceeds the threshold value, then natural mortality occurs and the number of surviving stems per ha at age A_2 is estimated by the algebraic difference form of the mortality model; otherwise natural mortality does not occur and the number of surviving stems per ha at age A_2 equals the initial number of surviving stems per ha. The most logical choice of a threshold is the average observed mortality rate (Monserud & Sterba 1999) which, in this study is equal to 0.745.

In the stochastic approach, the predicted probability of mortality incidence is compared with a random number between 0 and 1. If the random number is less than $\hat{\pi}p(x)$, natural mortality occurs and the number of surviving stems per ha at age A_2 is estimated using the algebraic difference form of the mortality model; if not, then the prediction is for no natural mortality.

Model Evaluation

Performance of the whole mortality models based on the probabilistic two-step approach (Eq.4), the deterministic threshold and the stochastic approaches were evaluated using the validation data set, and scatter plots of observed and predicted numbers of surviving stems per ha were produced for each. A simple linear regression was fitted for each approach and the coefficients of determination were used to compare the observed and the predicted number of surviving stems per ha. The observed (N) and the predicted $(N^{\hat{}})$ values were related following the linear model: NbbN10^+=. If the mortality model estimated the number of surviving stems per ha correctly, the intercept (b_0) should not be significantly different from zero and the slope (b_1) should not be significantly different from one.

RESULTS AND DISCUSSION

Model for Predicting Probability of Mortality Incidence

The probability of mortality incidence in the stand was well explained by a logistic regression model. The model is appropriate for dealing with the binary nature of mortality data. In the logistic model for predicting the probability of a stand experiencing any mortality in a 1-yr period, the best set of explanatory variables was stand density, site index and stand age (Table 3). Other variables (basal area, dominant height) were also tested. However, these two variables were less significant for predicting the probability of mortality incidence (based on the probability level of 0.05) allowing these to be removed from the model. Variability of these variables, however, may have been incorporated in the main explanatory variables.

The selected model for predicting probability of mortality incidence in a stand is:

$$\hat{\pi}(x) = \frac{1}{1 + \exp(-(-2.9 + 0.001N_1 + 0.121S + 0.18A_1))}$$
 (5)

where A_1 is stand age at the initial measurement (yr), N_1 is number of stems per ha at age A_1 , and S is site index (m).

The positive coefficient for the number of stems per ha (stand density) indicates that for stands of a given age and site index the predicted probability of mortality incidence increases with increasing stand density due to more intense inter-tree competition. The degree of competition may influence the survival likelihood of each individual tree. In stands with high density, trees compete for limited physical space and resources such as light, water and soil nutrients (Peet & Christensen 1987). Some trees may fail the competition and die. The influence of this variable was also shown in other stand or tree mortality models (Woollons 1998, Yao et al. 2001).

Table 3. Parameter estimates, standard errors and related fit statistics of the selected model for predicting the probability of mortality incidence

Variable	Estimate	SE	Wald ² statistics	<i>p</i> -value
Intercept	-2.9	0.58	-5.07	0.000
Stand density (N_1)	0.0010	0.00037	2.85	0.004
Site index (S)	0.121	0.0290	4.15	0.000
Stand age (A_1)	0.18	0.055	3.29	0.001

The probability of mortality incidence in a stand also tends to increase with increasing site index, which is consistent with many previous studies (Eid & Tuhus 2001, Yao et al. 2001, Eid & Øyen 2003, Diéguez-Aranda et al. 2005). Yao et al. (2001) and Yang et al. (2003) explained that faster tree growth on better sites may lead to more severe competition and increased probability of mortality, especially for small trees. The faster growth in stand of higher site productivity also triggers competition-induced mortality at earlier ages (Oliver & Larson 1996). However, Vanclay (1994) criticized that high quality sites should support higher densities; therefore, stand mortality should be lower for given age and stand density. Woollons (1998) also found higher mortality on lower production sites. This could be attributed to the lower availability of water and certain nutrients, which might be the case on poorer sites (Jutras et al. 2003). For A. mangium, water availability may not be a problem as this species normally demands full light for good development and stunted when grown in shade (Lim et al., 2002). It may also be possible that the higher mortality on higher site quality as being partly an effect of higher local competition, coupled with a strong tendency of A. mangium to produce multiple leaders resulting in stand densities high enough to cause self-thinning in some plots, which cannot properly be accounted for by robust stand-level mortality models. Incorporating spatial competition measures may help in understanding and modelling this phenomenon, but it is beyond the scope of this study as spatial data are not typically available in forest inventory.

Probability of mortality incidence also increases with stand age. This seems to be

1100 1400

Number of stems per ha

1700 2000

0.2

explainable because the data were from unthinned stands, which often exhibit increasing mortality, particularly after 5 yrs from planting (Arisman et al. 2005). This result complies with the dynamic process of the competition and natural mortality of even-aged stands (Clutter et al. 1983, Gadow & Hui 1999).

The mean predicted probabilities of mortality incidence (at least one stem dying in a plot) with respect to number of stems per ha, site index and stand age in A. mangium stands generally coincide with the mean observed mortality within each class, despite the occasional discrepancies (Figure 1). The differences between mean values of the predicted and the observed probability of mortality mainly occurred in the smallest and the largest classes of each stand variable, where there were small numbers of observations. Irregular or stochastic conditions that may apply during the measurement periods may have also contributed the lower or higher predicted mortality incidence than observed. For all observations of all plots, the mean predicted probability of mortality incidence was 71.9%, while the actual incidence was 72.8%.

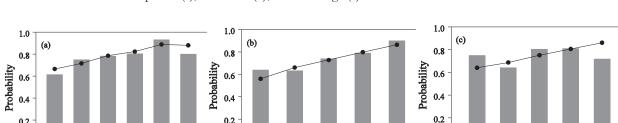
Models for Predicting Stand Density

0.0

2

23

The final parameter estimates for the nine fitted models as well as their standard errors (SE), t-statistics, p-values for significance testing, model root mean squared error (RMSE), and adjusted coefficient of determination (R^2_{adi}) are presented in Table 4. All models produced similar fits with values of RMSE and R^2_{adj} almost identical. All parameter estimates were found to be highly significant (p = 0.01), except for parameter c_0 in Model M8 and parameter c₁ in Model M9. The R_{adj}^2 for all models were generally high (> 94%),



14

11

17

Site index (m)

20

Figure 1. Predicted (line) and observed (bar) probability of mortality incidence computed for three stand variables: number of stems per ha (a), site index (b), and stand age (c).

10

Stand age (years)

compared with other studies for similar models producing R^2_{adj} for only 16-50% (Fridman & Ståhl 2001, Eid & Øyen 2003, Pothier & Mailly 2006). The *RMSE*s were relatively high at about 60 stems per ha (6.5%) over a period of 1 - 2 yrs. This can be explained by the occurrence of irregular mortality during the measurement periods that may also contribute to the model's errors. However, this is not unusual for mortality models emphasizing the fact that mortality is a complex and fairly unpredictable process for which there are many interrelated causes (Waring 1987).

Among the models that did not include site index as explanatory variable (Models M1, M2, M3, M5 and M8), Model M3, which assumes mortality rate is a power function of age performed slightly better than the others. This model is similar to Model M2 which was recommended by Woollons (1998) but his model included only one parameter. Model M1 proposed by Clutter *et al.* (1983) in which mortality rate is a constant proportion for all ages, site indices and stand densities does not appear to be suitable to this study. Its validation performance was inferior to all the others.

The inclusion of site index as an explanatory variable slightly improved the fits in all models as shown by Models M4, M6, M7 and M9. Model M7 proposed by Bailey *et al.* (1985) generally

performed better than Models M4, M6 and M9. Although Model M7 provided good fit, when it was used for projecting number of stems from age 1 to age 2 yrs it predicted an increase in the number of stems per ha, which was clearly illogical. This model should only be used for projecting survival from starting ages of 2 yrs or later. A similar problem occurs for Models M5 and M6, which also assume mortality rate is proportional to a hyperbolic function of age. Due to this limitation, the models that assume mortality rate is proportional to a hyperbolic function of age were rejected.

Models that consider the relative rate of change in the number of stems is proportional to an exponential function of age (Models M8 and M9) performed worst in terms of overall bias. One of the parameter estimates of each of these models was also not significant (p > 0.05). Although this type of model has been shown to be more accurate than others for *Pinus radiata* stands (González et al. 2004), it was less appropriate for A. mangium in this study.

In general, the models that consider the relative rate of change in the number of stems is proportional to a power function of age (Models M2, M3 and M4) seem to be most suitable. These models behaved logically and fitted the data well. Similar results were reported by Diéguez-Aranda

Table 4. Final parameter estimates, standard errors and related fit statistics of the fitted models for predicting stand density.

Model	Parameter	Estimate	SE	t	<i>p</i> -value	RMSE	R^2_{adj}
Mortality rate	is constant, indepe	endent of age:					
M1	c_0	-0.0539	0.00292	-18.45	0.000	61.010	0.946
Mortality rate	is proportional to	a power function	n of age:				
M2	c ₀	0.65	0.036	18.36	0.000	60.221	0.947
M3	b_2	1.31	0.182	7.19	0.000	59.896	0.948
	c_0	0.15	0.056	2.69	0.007		
M4	b_2	1.29	0.184	7.03	0.000	59.401	0.949
	c_1	0.0078	0.00292	2.68	0.004		
Mortality rate	is proportional to	a hyperbolic fun	ction of age:				
M5	b_1	0.13	0.041	3.18	0.002	60.508	0.946
	c_0	-0.077	0.0079	-9.78	0.000		
M6	b_2	0.09	0.037	2.52	0.009	60.321	0.947
	c_1	-0.0038	0.00038	-9.97	0.000		
M7	b_2	0.15	0.040	3.79	0.000	58.748	0.949
	c_0	-0.043	0.0082	-5.27	0.000		
	c_1	-0.003	0.0043	-6.21	0.000		
Mortality rate	is proportional to	an exponential f	unction of age:				
M8	b_2	1.064	0.0275	38.65	0.000	60.710	0.946
	c_0	-0.6	0.35	-1.70	0.090		
M9	b_2	1.057	0.0276	38.32	0.000	60.388	0.947
	c_1	-0.037	0.0236	-1.56	0.119		

et al. (2005) for mortality model of Pinus sylvestris. Within this group, however, Model M4 which includes site index was the best. Therefore, this model was selected for estimating the number of surviving stems per ha for A. mangium stands in this study. The final model (fitted from plots where mortality has occurred from the entire data set) is:

$$\hat{N}_2 = \left(N_1^{-0.5} + 0.011S\left(\left(A_2/100\right)^{1.47} - \left(A_1/100\right)^{1.47}\right)\right)^{-2} \tag{6}$$

Performance of the Selected Mortality Model

Scatter plots of the observed and predicted values of the number of surviving stems per ha were produced for the three different approaches and a simple linear model was fitted for each (Figure 2). In general, the three different approaches produced no aberrant results and the coefficients of determination were very similar (0.975 - 0.980). The test also revealed that the predicted number of surviving stems per ha of the three approaches was not significantly different from the observed number of surviving stems per ha (p > 0.30). All approaches should provide satisfactory predictions of the number of surviving stems per ha.

The overall biases at the projection ages were generally small, and were not significantly different from zero. All methods predicted the number of surviving stems per ha reasonably well. Some discrepancies between the observed and the predicted number of surviving stems per ha at the projection ages were found for the highest density class. Prediction problems in the highest density class were not unexpected since few sample plots were available at densities higher than 1500 stems per ha and this is probably of little practical concern because stand density in operational *A. mangium* stands typically does not exceed this number.

The stand mortality models developed in this study can be used for predicting stand density through either deterministic or stochastic approach. Deterministic prediction based on the probabilistic two-step approach assumes that the incidence of mortality over the plots or stands will be affected equally according to the stand conditions. The deterministic use of the model in this way will smooth values of mortality trend for the plots or stands. However, with a reasonably large number of plots, the prediction of mortality will still be unbiased at the stand level or even at the forest level (Eid & Øyen 2003). The threshold deterministic approach would avoid this "smoothing" values but it always produces the same estimate of stand mortality for a fixed threshold value (Diéguez-Aranda et al. 2005).

In real situations, mortality occurrence in the plots having the same growing conditions may not be the same due to the stochastic nature of tree mortality. In order to mimic the real situation more closely, the model may be used stochastically, despite it is having been developed for deterministic use. The probability of mortality incidence for a particular plot may be predicted from Eq. (6), and a random number distributed uniformly between 0 and 1 is used to determine whether or not the mortality occurred in the plot. The stochastic approach is, however, an alternative that allows different estimates for the same stand depending on the random number generated. The use of a random number may be a reasonable approach to deal with the fact that mortality is a stochastic phenomenon. This assumption may be more useful when the mortality model is used for large-scale management simulation, taking into account the stochastic nature of tree death (Woollons 1998).

Another alternative is to fit a model for predicting stand density as has been applied in the

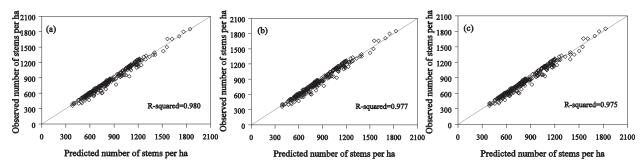


Figure 2. Scatter plots of observed and predicted number of surviving stems per ha using three different approaches: probabilistic two-step approach (a), deterministic threshold approach (b), and stochastic approach (c).

second step but including all plots with and without mortality incidence. The use of this one-step modelling approach fitted to all data may be a good alternative when natural mortality is frequent, as may occur in unthinned dense stands. However, this approach may create a problem when no actual mortality is observed in many plots (Woollons 1998, Eid & Øyen 2003). This approach was also tested in this study (results not shown), but some departure from normality and presence of large bias in prediction were indicated, which was consistent with the result of Woollons's study.

Weber et al (1986) and Vanclay (1991a) compared the deterministic and stochastic approaches in predicting mortality and could not find significance difference in their predictions. However, Belcher et al. (1982) noted that a stochastic approach typically predicts high mortality during some years and very little mortality in others. Such patterns may be more representative of actual events over short time periods, but they may inflate the variance of predictions over long projection periods (Pothier & Mailly 2006). Consequently, the deterministic prediction based on the probabilistic two-step approach was preferred to a stochastic approach for the application in this study. This approach has also been shown to be most accurate among the three approaches tested and thus should provide reliable prediction when it is to be used in forest productivity prediction and management system.

CONCLUSIONS

A two-step modelling strategy was used to develop a natural mortality model for *A. mangium* stands. The probability of mortality incidence for 1-yr period in the first step is mainly influenced by stand density, site index and stand age. The estimates of the probability of mortality incidence increase with increasing stand density, site index and stand age. At the second step, the best model for estimating stem number reduction due to mortality was the model that included site index as explanatory variable, in which the relative rate of change in the number of stems was proportional to a power function of age.

From the three different methods proposed for projecting the number of surviving stems per ha (i.e. probabilistic two-step, deterministic threshold and stochastic approaches), all methods provided similar results and reliable predictions. No important biases between the observed and the predicted number of surviving stems per ha were found. For inclusion in the forest productivity prediction system, however, the probabilistic two-step approach produces consistent and the most accurate estimates.

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