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ENVIRONMENTAL MANAGEMENT & CONSERVATION | RESEARCH ARTICLE

Density-dependent mortality in *Taiwania cryptomerioides* and *Chamaecyparis formosensis* stands in Taiwan

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Abstract: Taiwania (*Taiwania cryptomerioides* Hayata) and red cypress (*Chamaecyparis formosensis* (Matsum.)) are two red-listed species found mostly in Taiwan. A better understanding of the mortality patterns is necessary for good forest management of taiwania and red cypress, which is critical given that they are vulnerable and threatened species, respectively. The data for this project come from thinning trials where high-density plantations were established and later thinned. Mortality due to thinning was not included in the analysis. The mortality data were fitted to an exponential function using a negative binomial distribution model under a finite mixed modeling framework with stand density measures as predictor variables. The negative binomial distribution was zero-inflated for red cypress. Maximum mortality rates were fitted to the same exponential function used to model the mean response. Generally, average and maximum mortality rates increased as stand density increased, with stocking and average tree basal area having a large influence on mortality. Mortality rates were higher for red cypress than for taiwania. The differences in mortality rates could be due to the species

ABOUT THE AUTHORS

Chiu's major research interests are intensive management (thinning and pruning) of plantations, the qualitative and quantitative evaluations of stands, simulating growth and harvest yields with mathematical modeling and operational research, and formulating and evaluating the strategic planning of stand management operations models. Knowledge about self-thinning assists him with understanding stand dynamics and formulating silviculture plans.

Chien's major research area is seed biology and silviculture of trees and other woody plants. He performs research on (1) seed germination, seed storage and problems with seed dormancy of woody plants and (2) seed propagation with the objective of improving seedling quality. The self-thinning work will help in understanding the increase in forest tree seed production and seed quality to obtain high-quality seedlings through natural regeneration from these thinning stands.

Nigh's major research areas are in growth and yield modeling, site productivity, and relating climate to tree growth.

PUBLIC INTEREST STATEMENT

One common cause of tree death is through self-thinning, that is, the trees die through overcrowding and a lack of resources that are needed to grow, which are mainly moisture, sunlight, and nutrients. As the number of trees in a forest stand increases, the competition between trees for these resources increases. The competition also depends on tree size. Our research investigates the rates at which trees die due to overcrowding. This allows foresters to plan tree harvesting operations to extract the trees before they die to use as valuable products such as lumber. Our work also quantifies natural mortality rates. We observed mortality rates from 0 to over 2000 trees per hectare per year. Therefore, observing large number of dead trees in these types of forests is not unusual.

relative shade tolerance or their ability to withstand competition. The mortality models can be used for developing thinning prescriptions and managing these species for conservation.

Subjects: Conservation—Environment Studies; Ecology—Environment Studies; Resource Management—Environmental Studies

Keywords: boundary line; conservation; finite mixture models; frontier line; negative binomial; self-thinning; threatened; vulnerable; zero-inflated

1. Introduction

The coniferous tree species taiwania (*Taiwania cryptomerioides* Hayata) and red cypress (*Chamaecyparis formosensis* (Matsum.)) are endemic to Taiwan. Red cypress grows naturally in the northern and central mountains of Taiwan at moderate to high elevations (800–2,800 m with most stands in the 1,500–2,150 m range) (Mu, Luo, Chang, Huang, & Shi, 2013). It is a large species, reaching heights up to 65 m and diameters of 6.5 m (Huang et al., 1994). Red cypress grows in pure stands or mixed with *C. obtusa* and other conifers (Huang et al., 1994). Taiwania is found in the central mountains at elevations from 1,800 to 2,600 m. It is also a large species and attains heights up to 60 m and diameters from 2 to 3 m (Huang et al., 1994). In Taiwan, taiwania is usually found scattered mainly with *Chamaecyparis* spp., but also with other conifers. It is also found on mainland China and in lesser amounts in Myanmar and Viet Nam (Huang et al., 1994; International Union for Conservation of Nature & Natural Resources, 2014). Both red cypress and taiwania are very long-lived species and can attain ages over 1,500 years.

According to the International Union for Conservation of Nature and Natural Resources (2014), both of these species are red-listed; taiwania has a status of vulnerable and red cypress is endangered. Both species have valuable wood, which has led to their over-harvesting. The population of taiwania has stabilized due to conservation measures in Taiwan. However, the population of red cypress is still in decline, especially for old-growth stands. Managing for sustainability will help keep these species from further decline.

Mortality in forest stands is one of the least understood processes in forest ecology and is difficult to predict due to its high variability, but plays an important role in forest stand dynamics (Bigler & Bugmann, 2004; Franklin, Shugart, & Harmon, 1987; García, 2009; Oliver & Larson, 1996; Taylor & MacLean, 2007; Weiskittel, Hann, Kershaw, & Vanclay, 2011). Mortality is caused by a myriad of factors, some of which may interact, including senescence, insect attack, disease, wind, fire, drought, intra- and inter-specific competition, and harvesting. Mortality is classified as regular or irregular. Regular mortality is due to competition for light, nutrients, moisture, and growing space while irregular mortality is caused by factors that are stochastic in nature, usually catastrophic, and are independent of stand density (Álvarez González, Castedo Dorado, Ruiz González, López Sánchez, & von Gadow, 2004; Lee, 1971; Pothier & Mailly, 2006). Regular mortality is considered to be predictable (Pothier & Mailly, 2006) and is usually included in growth and yield models. Irregular mortality is also sometimes included in models as a stochastic event (Liu & Ashton, 1995).

Density-dependent mortality is the process whereby the resources available for plant growth are limiting and mortality must occur in order for stands to develop (Hamilton, Matthew, & Lemaire, 1995). The mechanism for density-dependent mortality is thought to be largely due to competition for light, as opposed to competition for nutrients (Gafta & Crişan, 2010; Hamilton et al., 1995; Weiskittel, Gould, & Temesgen, 2009). Density-dependent mortality is often used synonymously with the term self-thinning (e.g. Ellison, 1989; Lonsdale, 1990). However, it has been noted that mortality related to causes other than competition can also be affected by density, especially in mixed species stands (McCarthy-Neumann & Kobe, 2008; Piao, Chun, Yang, & Cheon, 2014; Wright, 2002).

The objective of this project was to develop models to predict average and maximum mortality rates in high-density stands of taiwania and red cypress due to natural causes (therefore, mortality from harvesting is not considered) over a range of stand densities. This information is important to forest managers because it provides necessary information for the calculation of forest yield and for allocating resources on tending and protecting forests (Franklin et al., 1987), which is particularly important for the two red-listed species under consideration.

2. Data

The data for this project came from three sites: Tengzhih and Liukuei (taiwania), and Chilan Mountain (red cypress).

2.1. Tengzhih (Taiwania)

The Tengzhih site (longitude 120º 45' 44", latitude 23º 10' 19") is in Kaohsiung City in south-central Taiwan. It is at an elevation of 1,300 m and has a mean annual temperature of 17.2 °C and annual precipitation of 3,000 mm. This test site was established in 1,967 at 2,500 stems per ha and was thinned at age 17 and again at age 25 to three levels (light, medium, and heavy) and the controls (Chiu, Nigh, Chien, & Ying, 2010). The first thinning left a basal area of 51, 46, 41, and 59 m²/ha and the second thinning left a density of 1,000, 800, 600, and 1500 stems per ha for the light, medium, heavy, and controls, respectively. The first measurement was taken at age six and the plots were re-measured at four–six year intervals. There were 6 plots per treatment and each plot was 0.06 ha.

2.2. Liukuei (Taiwania)

The Liukuei site (longitude 120º 42' 51", latitude 23º 00' 14") is also in Kaohsiung City and is at an elevation of approximately 1,550 m, with a mean annual temperature of 18.6 °C and annual precipitation of approximately ,2200 mm. There were three installations at the Liukuei site. The compartment 3 installation was planted in 1972 and thinned to three levels and the controls at ages 14 and 31, leaving 1,300, 1,125, 975, and 1980 stems per ha at age 14 and 800, 600, 425, and 1730 stems per ha at age 31. The first measurement was at age 9 with an irregular re-measurement interval of mostly between 1 and 3 years until age 39. There were 4 plots per treatment with a plot size of 0.04 ha. The compartment 12 installation was planted in 1979 and thinned once at age 11 to two levels of basal area (27.5 m²/ha, 32.5 m²/ha) and a control (42 m²/ha). The first measurement was taken at age 11 and the plots were re-measured annually until age 17, then at every 4–6 years until age 32. Compartment 12 had 12–0.04 ha plots per treatment. A third installation consisted of one plot in an older plantation that was established in 1938 and had no treatments during the measurement period. The plot was measured at ages 66, 68, 71, and 75.

2.3. Chilan Mountain (Red cypress)

The red cypress data came from a thinning experiment at Chilan Mountain in northern Taiwan (longitude 121º 29' 29", latitude 24º 37' 04"). This site was at an elevation of 1,100 m, with a mean annual temperature of 13 °C and an annual precipitation of 4000 mm. The plantations were established at 10,000 stems per ha in 1980. By age 8, significant mortality had occurred and the stand densities were thinned to 5,000, 2,500, 1,660, and 1,100 stems per ha. The control plots were left at a density of approximately 8600 stems per ha at that time. The height and diameter of the trees were measured annually for 9 years starting at age 8, then at 4–5 year intervals until the last measurement at age 30. There were 6 plots per treatment and the plots were 0.02 ha.

At all test sites, the measurements consisted of diameter at breast height (dbh, cm) and height (m). Trees removed by the thinning treatments were identified so that both pre- and post-thinning densities could be determined. Stocking (trees/ha), average tree basal area (m²/tree), and stand basal area (m²/ha) were calculated from the data. Statistics for these variables are given in Table 1 for both species. The taiwania plots generally had lower stocking, larger trees, and greater stand basal areas than the red cypress plots. They also had lower rates of mortality than did the red cypress plots. No ingrowth was recorded on any of the plots.

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Table 1. Summary statistics for the taiwania and red cypress data				
Species	**Variable**	**Mean**	**Minimum**	**Maximum**
Taiwania	Mortality (trees/ha/yr)	6	0	225
	Stocking (trees/ha)	1216	221	2500
	Mean tree basal area (m²/tree)	0.051	0.005	0.424
	Stand basal area (m²/ha)	53.2	8.1	101.6
Red cypress	Mortality (trees/ha/yr)	133	0	2350
	Stocking (trees/ha)	2966	900	9450
	Mean tree basal area (m²)	0.014	0.001	0.047
	Stand basal area (m²/ha)	29.4	6.2	59.9

3. Methods

The focus of this study is mortality, which we define as the annual change in trees per ha due to natural mortality. We hypothesized that mortality was driven by, and hence related to, stand density. We chose variables stocking (trees/ha, tph), average tree size expressed as basal area/tree (m²/tree, ave_ba), and their interaction (product) which is stand basal area (m²/ha, stand_ba) as measures of density because tree size or number alone is not an adequate measure of density (Zeide, 1988). A model that predicts annual mortality (annual change in stocking) from the stocking, tree size, and stand basal area at the beginning of the measurement period was developed to test our hypothesis. Mortality due to the thinning treatments was not included in the analysis since thinning mortality did not meet our definition of natural mortality. Therefore, for the measurements when a thinning occurred, the pre-thinned data were used to calculate the response variable (mortality rate) for the preceding measurement period and the post-thinned data were used to calculate the response variable and predictor variables for the succeeding measurement period. Figure 1 is a plot of the mortality rates versus stocking and average tree basal area for the taiwania and red cypress study plots.

We proposed an exponential model for describing the relationship between mortality and stocking, tree basal area, and stand basal area. This model for each plot is:

$$E[mort] = offset \times e^{a_0 + a_1 \times tph + a_2 \times ave\_ba + a_3 \times stand\_ba}$$

(1)

where mort is the number of trees in a plot that died over the measurement interval, tph is stocking at the beginning of the measurement period, ave_ba is the average basal area of the trees at the beginning of the measurement period, stand_ba is the interaction of tph and ave_ba and equals total basal area per ha, and E is the expectation operator. The parameters to be estimated are a_0, a_1, a_2, and a_3. The annual mortality rate (trees/ha/yr) is predicted by $e^{a_0 + a_1 \times tph + a_2 \times ave\_ba + a_3 \times stand\_ba}$. The variable offset is referred to as exposure or the offset in the statistical literature (McCullagh & Nelder, 1992). In this case, it accounts for the different plots sizes and measurement intervals by scaling the annual mortality rate into the same scale as the observed tree counts (mort). Offset is equal to the measurement interval multiplied by the plot size.

Standard linear regression techniques are not appropriate for fitting this model because the standard assumptions for regression (Affleck, 2006; Sen & Srivastava, 1990) will not be met. In particular, the assumption that mort is normally distributed is violated because it can only take on nonnegative integer values and is discrete.

The response variable in our model, which is the number of trees that died, is a count variable. The Poisson and negative binomial distributions are classical probability models for count data (Hu, Pavlicova, & Nunes, 2011). Furthermore, there appears to be a large number of observations with zero mortality. Therefore, four non-normal regression models were proposed that are appropriate

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Figure 1. Fitted relationship between the mean mortality rate and the variables stocking and average tree basal area for taiwania (part a) and red cypress (part b) overlaid on the mortality data (dots).
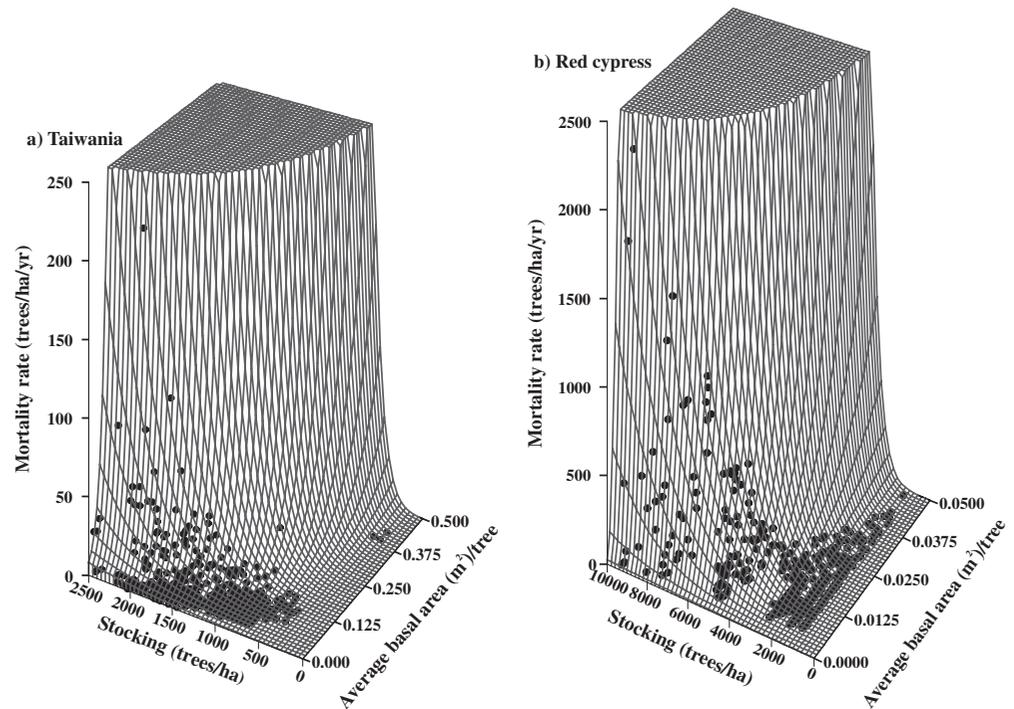
for our mortality data: Poisson, negative binomial, and, to account for the large number of plots with no mortality, their zero-inflated counterparts (Statistical Consulting Group, 2007; Hu et al., 2011). The Poisson model has the mean, given by equation 1, as the only parameter and the data are assumed to follow a Poisson distribution. The variance equals the mean for this distribution. The negative binomial model has two parameters: the mean (given by equation 1) and the scale (scale > 0), and the data are assumed to follow a negative binomial distribution. The variance of the negative binomial distribution is mean + scale × mean², so the variance for this model is greater than the mean. The zero-inflated counterparts to these models are mixture models because they have two component distributions representing data from two sub-populations: the Poisson or negative binomial distribution and a degenerate distribution. The degenerate distribution has all the mass concentrated at one value (0 in this case) and consequently an observation from this distribution always takes the value of 0, that is, the probability of mortality is 0 for this observation. The probability that the observation comes from one sub-population or the other is known as the mixing probability and can be constant or it can be a function of covariates.

We fit the models with procedure FMM (Finite Mixture Models) in SAS/STAT (SAS Institute Inc, 2011). FMM has a wide variety of built-in parametric distributions including mixture distributions such as the zero-inflated Poisson and negative binomial. A variety of link functions for the mixing probabilities are available in procedure FMM; we chose the link function and that provided the best fit to the data using the variables in equation 1. We found that the link function that provided the best fit is the logit function (2):

$$P_{NB} = \frac{e^{c_0 + c_2 \times ave\_ba + c_3 \times stand\_ba}}{1 + e^{c_0 + c_2 \times ave\_ba + c_3 \times stand\_ba}} \tag{2}$$

where P_{NB} is the probability that the observation is from the negative binomial distribution (as opposed to being from the degenerate zero-distribution), the c_i, $i = 0, 2,$ or 3, are parameters that are estimated, and all other variables are as previously defined.

The two distributions being fit and the link function are specified by the user. Procedure FMM builds the mixture distribution and model fitting is done by maximum likelihood. Note that in the mixture model formulation, the mean function (equation 1) only applies to the observations from the Poisson or negative binomial sub-population. Model fit was evaluated with the Akaike Information Criteria (AIC) (Burnham & Anderson, 1998). All variables in the model were assessed for their contribution to the fit by removing them from the model one-at-a-time and if the AIC increased, the variable was deemed to be unnecessary and remained excluded from the model.

The maximum mortality rate (trees/ha/yr) was also modeled. The predictions from standard regression techniques represent the average response conditional on the value of the predictor variable(s). However, for the maximum mortality models we desired the maximum value of the response, otherwise known as the frontier (or boundary) line (surface). The frontier line is a line below which most observations occur (Aigner, Lovell, & Schmidt, 1977; Cardiel, 2009; Zhang, Bi, Gove, & Heath, 2005). Commonly, frontier lines are fit by modifying the error term (e.g. Aigner et al., 1977; Cardiel, 2009). We chose an alternative method as described below because our fitted models allowed us to derive pseudo-data for each species, namely the estimated 99.5th percentile for each observation, from which we were able to fit a frontier surface. This was done by first using the estimated parameters from the fitted distribution of counts and calculating the cumulative probability of observing k trees dying for each observation, where $k = 0, 1, 2$, and so on. K was incremented until this cumulative probability just exceeded 0.995. The value of k at this point is the 99.5th percentile. We could have stopped there but we also wanted a predictive equation for this upper frontier. Therefore, Model 2, which has the same functional form as the final fitted mean models for the respective species, were then fit to these percentiles using nonlinear least squares [procedure NLIN in SAS/STAT (SAS Institute Inc, 2011)]. Nonlinear least squares were used for model fitting because the model is nonlinear in the parameters and otherwise is straightforward in terms of fitting.

$$(3)$$

$$\text{mort}_{\text{fron}} = e^{b_0+b_1\times tph+b_2\times ave\_ba+b_3\times stand\_ba}$$

where $\text{mort}_{\text{fron}}$ (trees/ha/year) is the annual rate of mortality at the frontier, b_0, b_1, b_2, and b_3 are parameters to be estimated, and all other variables are as previously defined. Note that for taiwania, the term $b_2 \times ave\_ba$ was removed from the model because the final fitted model for the mean response for taiwania did not include it.

The fit of the mean annual mortality models was tested as follows. For each observation, the expected value of the number of trees dying per ha per year is predicted using the best-fitting model. These values were binned into the following classes: 0, 1 – 5, 6 – 10, . . ., 91 – 95, 95 + (for taiwania); 0, 1 – 100, 101 – 200, . . ., 1801 – 1900, 1901 + (for red cypress). The predicted number of observations in each bin class was divided by the total number of observations to give a proportion of observations in each class. The same process was followed for the observed number of trees dying after converting the raw data into trees per ha per year. A histogram of the predicted and observed mortality rates in each class was then produced to facilitate an evaluation of the overall fit of the models.

4. Results
The results of the mean mortality models are in Table 2 and the results of the analysis of the mortality frontier are in Table 3.

4.1. Taiwania
The negative binomial distribution with predictor variables tph and stand_ba provided the best fit of model 1 to the taiwania data. The mean of the fitted model is given by:

$$\text{mort} = e^{-1.0842+0.001285\times tph+0.02034\times stand\_ba}.$$

Table 2. Results of the analysis of the mean mortality model (model 1 with mixing probability functions 3 and 4). Parameters a_0 to a_3 are from the mean mortality model, parmaeters c_0 to c_3 are for the mixing probabiltiy function, and scale is a overdisperson parameter

Species	Parameter			Number of observations	AIC
	Name	Estimate	Standard error		
Taiwania	a_0	−1.0842	0.2991	683	1497
	a_1	0.001285	0.0001591		
	a_3	0.02034	0.003262		
	scale	1.3452	0.1839		
Red cypress	a_0	3.0228	0.3743	360	1356
	a_1	0.0002822	0.00004623		
	a_2	−77.6569	12.8961		
	a_3	0.05465	0.008891		
	scale	0.4125	0.06839		
	c_0	−2.5927	0.6639		
	c_2	−94.5792	29.6096		
	c_3	0.1823	0.02929		

Table 3. Results of the analysis of the frontier line for mortality (model 2)

Species	Parameter			Number of observations
	Name	Estimate	Standard error	
Taiwania	b_0	0.9030	0.002199	683
	b_1	0.001239	0.0000009072	
	b_3	0.01967	0.00002089	
Red cypress	b_0	4.1423	0.006928	360
	b_1	0.0002823	0.0000006748	
	b_2	−79.4028	0.4644	
	b_3	0.05770	0.0001231	

and the fitted frontier surface is:

$$\text{mort}_{\text{fron}} = e^{0.9030 + 0.001239 \times \text{tph} + 0.01967 \times \text{stand\_ba}}$$

Mortality increases as stocking and average tree size increase (Figure 1a). Mortality is negligible at very low stocking levels regardless of average tree size. However, mortality rates increase significantly when densities reach 2500 stems per ha, even when the average tree size is small. A similar pattern is seen in the mortality frontier (Figure 2a).

Figure 3a shows a close correspondence between the observed and predicted mean mortality rates, indicating the model is a good fit to the data.

4.2. Red cypress

The zero-inflated negative binomial distribution with all three predictor variables in the mean function and variables ave_ba and stand_ba in the logit mixing probability function provided the best fit of model 1 to the red cypress data. The mean mortality model for red cypress for the sub-population undergoing mortality is:

$$\text{mort} = e^{3.0228 + 0.0002822 \times \text{tph} − 77.6569 \times \text{ave\_ba} + 0.05465 \times \text{stand\_ba}}\cdot$$

Figure 2. Fitted mortality frontiers plotted against stocking and average tree basal area for taiwania (part a) and red cypress (part b) overlaid on the mortality data (dots).
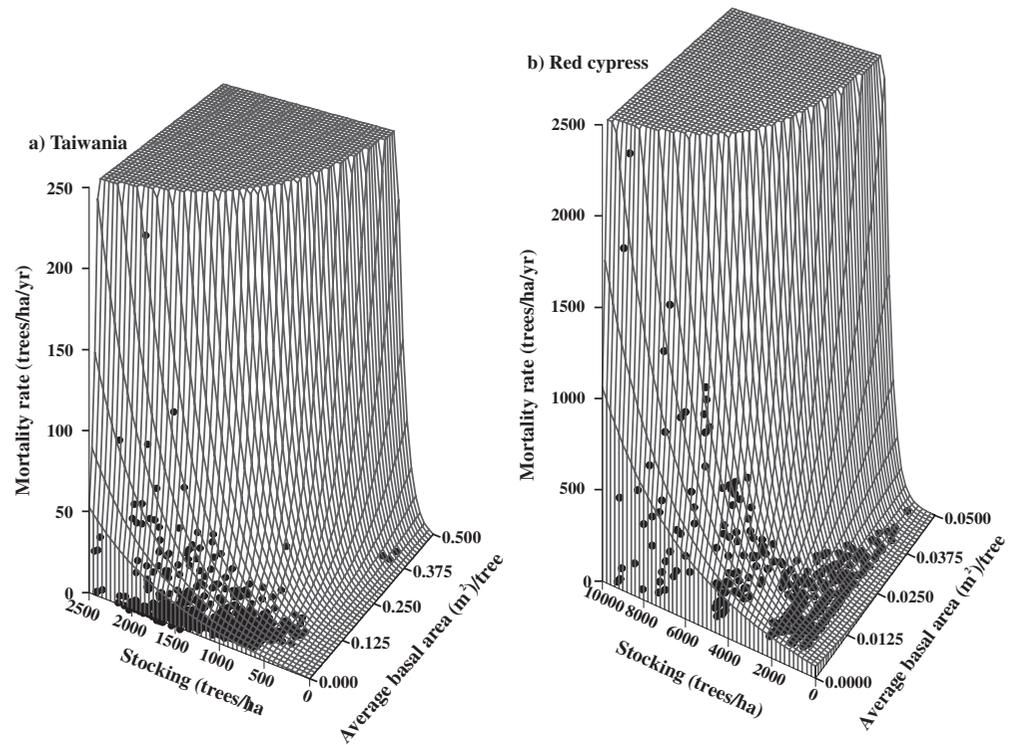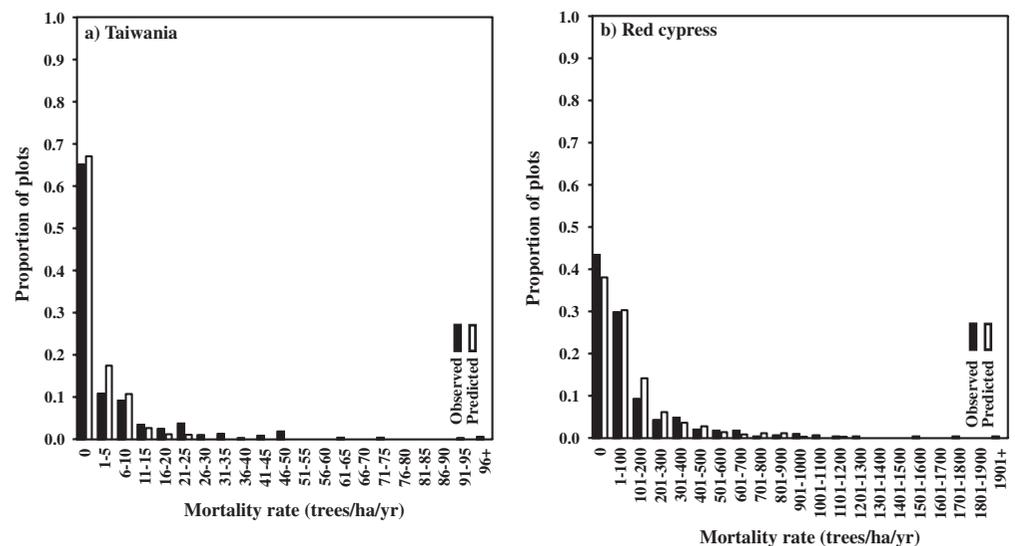

Figure 3. Histogram of the proportion of observed and predicted number of plots in each mortality rate class for taiwania (part a) and red cypress (part b).


and the estimated mixing probability function is:

$$P_{NB} = \frac{e^{-2.5927-94.5792 \times ave\_ba + 0.1823 \times stand\_ba}}{1 + e^{-2.5927-94.5792 \times ave\_ba + 0.1823 \times stand\_ba}}$$

The predicted mixing probabilities for red cypress are plotted in Figure 4. At low levels of stocking, the mixing probability decreases as average tree basal area increases. However, at stocking levels above approximately 400 stems per ha, the mixing probability increases as average tree size increases. The mixing probability increases as stocking increases and rapidly approaches a value of 1.0.

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Figure 4. Mixing probabilities vs. stocking and average tree basal area for red cypress.
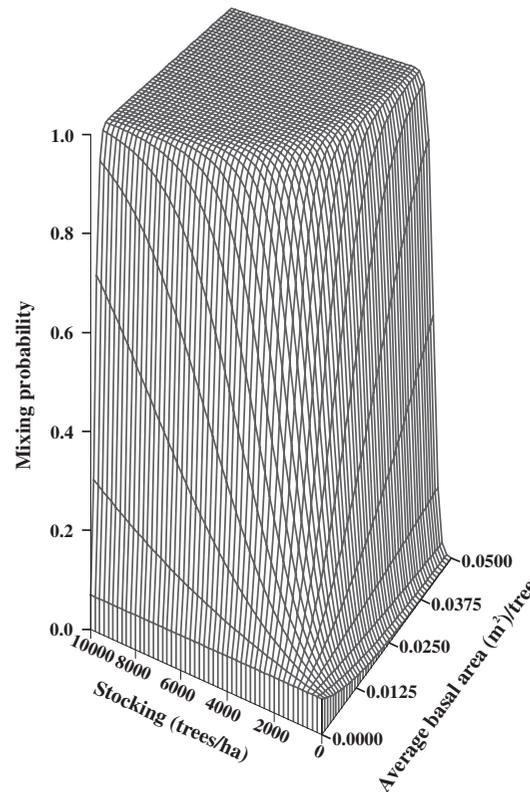
Mortality for the whole population is obtained by taking the expected value of the mixture distribution. The probability that an observation came from the degenerate distribution (the no mortality sub-population) is $1 - P_{NB}$ and the expected value of the degenerate distribution is 0. Therefore, the above equation for mort is multiplied by the above equation for the mixing probabilities for red cypress to get the mortality rate for the population of red cypress as a whole.

The fitted mean mortality surface for the whole population is shown in Figure 1b along with the data. Red cypress mortality increases as both stocking and average tree basal area increase. Little mortality occurs below 2,000 stems per ha, but increases rapidly as stocking level increases.

The fitted mortality frontier surface for red cypress is:

$$\text{mort}_{\text{fron}} = e^{4.1423+0.0002823\times tph - 79.4028 \times ave\_ba + 0.05770 \times stand\_ba}$$

As with taiwania, the mortality frontier surface shows the same trend as the average mortality (Figure 2b).

The proportion of plots in each mortality class that were observed and predicted is given in Figure 3b. As with taiwania, there is excellent correspondence between the predicted and observed mortality rates within these classes. The model is a good fit to the data.

5. Discussion

Many self-thinning studies analyze data that have been summarized into yield tables or compiled into plot data (e.g. Lonsdale, 1990; Pretzsch, 2006; Weller, 1987; Zeide, 1987; Zhang, Oliver, & Powers, 2013). With this approach, details about individual tree mortality causes are lacking so it must be assumed that reductions in stems per ha are caused by self-thinning. However, it is very likely that other causes of mortality are extant in the data. The causes of endemic mortality for this project were not

identified at the time of data collection, although a few plots were identified as having catastrophic mortality. However, most of the study sites are young with high initial stocking and those plots with catastrophic mortality were excluded from the analysis. Therefore, we assume that mortality is largely due to self-thinning with small amounts of endemic mortality due to unknown factors.

Insight into the cohort of red cypress plots that are undergoing mortality can be obtained from the mixing probability function. Recall that observations from the red cypress sub-population represented by the negative-binomial distribution have a non-zero probability of mortality, whereas the observations from the degenerate distribution have a zero probability of mortality. The proportion of the red cypress population that comes from the mortality sub-population increases as both the stocking level and average tree basal area increase, except at low levels of stocking (Figure 4). At stocking levels of less than approximately 400 trees per ha, the proportion of plots with a non-zero probability of mortality decreases as average tree size increases. However, this proportion increases very rapidly to 100% as both stocking and average tree basal area increase. Since red cypress experiences high rates of mortality, especially compared to taiwania, reducing the probability of mortality may have great importance. Some management objectives, such as maximizing carbon sequestration, may require that mortality be reduced as much as possible. This objective could be met by managing stands such that the probability of experiencing mortality is small, i.e. the mixing probability is small. Reducing the probability of mortality could be done by adjusting stands so that they have low stocking levels, particularly as tree size increases. Note that regions of this mixing probability surface include conditions that are unlikely to occur, for example, a stand with 10000 trees per ha is unlikely to have an average tree basal area of 0.05 m^2 (approximately 25 cm dbh).

Since the taiwania mortality model is not a mixture model, we interpret that to mean that there is a non-zero probability of mortality at all levels of stocking and basal area. We conclude that red cypress is less susceptible to undergoing mortality than taiwania when the stocking is low and average tree size is small.

The influence of stocking and average tree size on the overall mortality rate can be determined from the mean mortality surfaces given in Figure 1. For both species, mortality increases as stocking and mean tree basal area increase. Given that the mixing probability for red cypress decreases as average basal area increases at low stocking levels, the mortality rate also decreases although this decrease is so small that it is not apparent on the graph at this scale (Figure 1b). Zhang, Lei, and Liu (2014) also found that mortality decreased as average tree basal area increased. They attributed this to a decrease in mortality as a stand ages. Decreasing mortality rates as average tree size increases does not occur for taiwania. The increase in mortality as stocking and average tree size increase is common and is usually a result of competition (Piao et al., 2014). For both species, there is very little mortality at low stocking levels for all observed average tree basal areas. However, the mortality rate increases rapidly as stocking increases regardless of tree size. Note that the range of mortality rates is approximately 10 times greater for red cypress than for taiwania. The range in stocking is four times larger for the red cypress data, while the range in average tree basal area is one-tenth.

While it is not easily discernable in the graphs, the mortality rate is generally higher for red cypress than for taiwania over the range of data observed in this study except when average tree basal area is very small. This will most likely occur in young stands and may indicate that initially red cypress tolerates competition at higher stocking levels better than taiwania or that competition sets in earlier for taiwania. As the stands mature, however, red cypress experiences much greater mortality than does taiwania. Mortality rates of less than 1% are expected to occur for both species if the stocking is kept below 1,000 trees per ha even at larger average tree sizes. Significant mortality will start to occur in red cypress stands as stocking levels increase above 1,000 trees per ha. Consequently, thinning may be necessary in well-stocked red cypress stands as basal area increases to reduce natural mortality. This may also be the case for taiwania stands, although the mortality rates for taiwania are much lower so it may not be as significant an issue as it is for red cypress.

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Both red cypress and taiwania have similar reproductive strategies. Red cypress reproduces poorly in mature forests and is considered to be a quasi-climax species that persists due to its longevity and ability to colonize disturbed areas (Hawk, 1976). Taiwania is similar to red cypress in that it also persists due to its longevity and regenerates after disturbance (International Union for Conservation of Nature & Natural Resources, 2014). The results of this analysis indicate that self-thinning would not occur in newly regenerated stands until the stands are well established for both species. Red cypress is semi-shade tolerant, but its best growth is realized at higher light intensities (Hawk, 1976; Hung & Lo-Cho, 1979; Lin, Lin, & Lu, 1958). Very little information about the shade tolerance of taiwania exists. However, Fang, Chiu, Liao, and Lin (1990) found that the survival of taiwania seedlings increased as light intensity decreased. The results of this study suggest that, when compared to red cypress, taiwania survival is greater in denser stands where more self-shading is occurring.

The mortality frontier surfaces depend on the stocking and stand basal area. The parameter estimates for the mean mortality model and the mortality frontiers are similar except for the intercept parameter in the linear equation in the exponent. Therefore, the frontier is essentially the mean surface that has been scaled up. These scaling factors are approximately 7.3 and 3.1 for taiwania and red cypress, respectively. That is, for taiwania the maximum mortality rate is 7.3 times the average mortality rate and is 3.1 times the average morality rate for red cypress. The graphs of the frontier models (Figure 2) show the same trends as the mean mortality models. For red cypress, the maximum mortality rate decreases as the stand basal area increases at low-stocking levels. At higher stocking levels, the maximum mortality rate increases as basal area and stocking increase. For taiwania, the maximum mortality rate increases as both stocking and stand basal area increase. The mortality frontier is greater for red cypress than it is for taiwania; again, this indicates that red cypress undergoes more self-thinning than does taiwania.

As well as being ecologically interesting, the mortality information from this research has practical purposes. A forest manager could use the information to assess the risk of high mortality rates, particularly in natural stands where high levels of stocking might exist. Thinning prescriptions for highly stocked stands could be devised to thin down to stocking levels with acceptably low mortality rates. Since mortality is a function of average tree basal area as well as stocking, the manager could target trees to be thinned to adjust stocking and average tree size to further reduce mortality. Planting densities could be established to minimize later mortality. The mortality models developed here would work well in individual-tree growth and yield models and also in stand-level models with stocking and average tree size as predictor variables.

6. Conclusion

Mean and maximum mortality rates in red cypress and taiwania stands are related to stocking (trees/ha), average tree basal area, and their product which is stand basal area. Generally, morality increases as average tree basal area and/or stocking increase and the mortality rates for red cypress are greater than for taiwania. This may be related to their relative shade tolerance or their ability to compete for growth resources. Both of these species are red listed as vulnerable or endangered, meaning that they are at risk of extinction. Consequently, it is critical that they undergo good management to avoid this fate. Knowledge about mortality provided by this work lends itself to achieving the continuance of these species.

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