Modeling stand-level mortality based on maximum stem number and seasonal temperature

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Abstract

Mortality is a key process in forest stand dynamics. However, tree mortality is not well understood, particularly in relation to climatic factors. The objectives of this study were to: (*i*) determine the patterns of maximum stem number per ha (MSN) over dominant tree height from 5-year remeasurements of the permanent sample plots for temperate forests [Red pine (*Pinus densiflora*), Japanese larch (*Larix kaempferi*), Korean pine (*Pinus koraiensis*), Chinese cork oak (*Quercus variabilis*), and Mongolian oak (*Quercus mongolica*)] using Sterba's theory and Korean National Forest Inventory (NFI) data, (*ii*) develop a stand-level mortality (self-thinning) model using the MSN curve, and (*iii*) assess the impact of temperature on tree mortality in semi-variogram and linear regression models. The MSN curve represents the upper boundary of observed stem numbers per ha. The developed mortality model with our results showed a high degree of reliability ($R^2 = 0.55\text{-}0.81$) and no obvious dependencies or patterns in residuals. However, spatial autocorrelation was detected from residuals of coniferous species (Red pine, Japanese larch and Korean pine), but not for oak species (Chinese cork oak and Mongolian oak). Based on the linear regression analysis of residuals, we found that the mortality of coniferous forests tended to increase with the rising seasonal temperature. This is more evident during winter and spring months. Conversely, oak mortality did not significantly vary with increasing temperature. These findings indicate that enhanced tree mortality due to rising temperatures in response to climate change is possible, especially in coniferous forests, and is expected to contribute to forest management decisions.

Keywords: *maximum stem number, temperate forest, tree mortality, national forest inventory, temperature, self-thinning*

1. Introduction

Tree mortality is key process in stand dynamics and a highly complicated process. It is affected by a variety of environmental, physiological, pathological, and entomological factors, as well as random events. Generally, tree death results from complex interactions among multiple factors and is often a gradual process, although it can sometimes be abrupt (Waring, 1987). Some factors weaken trees, while others directly cause tree death (Manion, 1981). Due to the complexity of the mortality process and uncertainty in the timing of tree death, mortality remains one of the least understood components of growth and yield estimation (Hamilton, 1990).

Although tree mortality is complicated, some generalities exist. There are two basic structures of mortality algorithms, deterministic and stochastic, and there are six types of mortality algorithms, including gap-type, statistically fitted, carbon-based, abiotic/age, competitive, and progressive-stress algorithms (Hawkes, 2000). The degree of competition especially influences the likelihood of survival of each individual tree (Dobbertin and Biging, 1998). Unless trees are grown in an open environment, they always experience some competition from their neighbors, depending on stand density and the size and location of the neighboring trees. Trees compete for limited physical space and resources, such as a light, water, and soil nutrients. Some trees are outcompeted and subsequently die. Therefore, variables that describe this competition are essential for mortality modeling. Most mortality algorithms are empirical-based (statistical fitted), while others are process-based (Hawkes, 2000).

The mortality models have also generally been classified as two groups, tree- and stand-level models (Landsberg and Sands, 2011). Tree-level models had relatively complex algorithms and more uses for modeling the dynamics of uneven-sized stands than stand-level models (Groot et al., 2004; Vanclay, 1994). Stand-level models have helped to forecast of forest resource conditions, as growth and yield in terms of volume, changes in order to obtain relevant information for sound decision making (Landsberg and Sands, 2011).

However, most models do not sufficiently meet the requirements of large-scale forestry scenarios applied to country or country-wide analyses on the property level. Some models are based on locally relevant, or insufficiently representative data, while others are adapted to certain treatments (e.g., only unthinned stands), and some account for only one or a few tree species of interest. For nation-wide analyses, the data should reflect the full range of variability with respect to treatments, sites, forest structure, and tree species. The use of data from a National Forest Inventory (NFI) with permanent sample plots is probably the best way to meet these requirements. For example, Monserud and Sterba (1999) developed a tree mortality model for Austrian forest species based on the Austrian NFI data.

Tree mortality is a natural ecological process (Franklin et al., 1987); however, drought- and heat-induced mortality, including associated infestation-related forest die-off, is often a selective force that differentially affects tree species and rapidly alters the size, age, and spatial structure of forests. Growing evidence suggests that many forests could be increasingly vulnerable to climate- and infestation-induced tree-mortality events (Allen et al., 2010; Hember et al., 2016). The significant interaction between climate and tree mortality for 11 common species, mainly pine and oak species, in Mediterranean regions was reported (Ruiz-Benito et al., 2013). Increased mortality are also associated with climate condition among many temperate tree species pine and fir species in central Turkey (Semerci et al., 2008), *Pinus tabulaeformia* in east-central China (Wang et al., 2007), *Abies koreana* in South Korea (Lim et al., 2008). Investigation into the physiological mechanisms through which dry and hot climatic conditions drive tree death and forest die-off represent a rapidly growing research area (McDowell et al., 2008; Sala et al., 2010), but the impact of forest die-off remains less well studied. Climate-induced forest mortality seems to be an emerging global phenomenon, yet there is very rare synthesis of the ecological, societal, and climatological consequences of dying forests at present.

The main goals of this study were to develop a model to simulate stand-level mortality (self-thinning) for temperate forests in South Korea and to evaluate the effect of the climate factor, in terms of temperature, on tree mortality. To achieve these objectives, permanent sample plots recorded by the Korean National Forest Inventory (NFI), Sterba's theory, semi-variogram analysis, and residual analysis were applied. The model is suitable both for even-aged as well as uneven-aged conditions.

2. Materials and methods

2.1 Description of South Korea forest and National Forest Inventory

South Korea forests occupy ~64% (6,450,438 ha) of total land area in the country. Evergreen needleleaf (mainly *Pinus densiflora*), deciduous broadleaf (mainly *Quercus* spp.), and mixed forests took up approximately 40.5%, 27%, and 29.3% of total forest area in 2015, respectively. South Korea's forest have been intensively managed and stocking volume has increased from 8.2 m^3 ha^{-1} in 1954 to 142.2 m^3 ha^{-1} in 2014 (Korea Forest Service, 2015). Currently, 69.5% of South Korean forests are less than 40 years old.

We used remeasurements from permanent plots of the Korean NFI for mortality and survival data (Korea Forest Service, 2015). A systematic 4-km grid of permanent plots covering South Korea was established in 2006–2010 (Korea Forest Research Institute, 2011). Each year, 20% of grid locations were sampled in a manner that the whole of South Korea was covered by the inventory each year. Each location was then remeasured from 2011–2015, exactly 5 years after the establishment. The total inventory comprises 4,200 clusters, consisting of 16,800 permanent plots. Four circular sample plots were located at the intersection of each 4 × 4-km grid line. Each sample plot (31.6-m radius) covered 0.16 ha. Forest characteristics (tree species, age, and height), diameter at breast height (*dbh*), number of trees with a diameter greater than 6 cm, and topographical factors (coordinates, elevation, slope, and aspect) were measured at all sites. Tree species identification of plots was determined according to basal area of the dominant species. If basal area of red pine occupied more than 75% in a plot, the plot was considered a "red pine" stand.

Stand-mortality of each plot was recorded during each measurement. Each tree in the permanent plot had a unique number and was checked to determine the vital status (e.g., live or dead). Through this process, the stand mortality in each plot was estimated. In addition, the vital status of each individual tree was recorded, with mortality from natural causes distinguished from normal harvesting and thinning. Therefore, some data showing natural (disease and insect pests, wind damage, landslide) or artificial (forest fires, illegal activities, land cover change) disturbances in the plots during 2006–2015 were not considered in this study.

In this study, we used the Korean NFI remeasured data and evaluated the status of more than 1,484 permanent plots of the five main temperate tree species in South Korea (Table 1), which include red pine (*Pinus densiflora*), Japanese larch (*Larix kaempferi*), Korean pine (*Pinus koraiensis*), Chinese cork oak (*Quercus variabilis*), and Mongolian oak (*Quercus mongolica*). These tree species form large forests in most of the mountainous areas of South Korea, occupying approximately 37%, 5%, 4%, 5%, and 11%, respectively, of the total forested area in 2010. Based on a sample of 1,484 permanent plots, the overall 5-year mortality rate is 16.2%, which corresponds to an annual rate of 3.2% yr^{-1} (Table 1). The most common species, red pine, has an annual mortality rate of 2.8% yr^{-1}. An annual mortality rates for other coniferous species vary between 5.2% yr^{-1} for Korean pine and 5.1% yr^{-1} for Japanese larch. Chinese cork oak and Mongolian oak were 4.2% yr^{-1} and 2.2% yr^{-1}.

<Table 1>

2.2 Stand-level mortality model

2.2.1 Background of self-thinning principles

Self-thinning principles were developed to explain tree mortality. According to Reineke's expression (Reineke, 1933) and the -3/2 power rule of self-thinning (Yoda et al., 1963), a log-log plot of the average tree size and stand density (stems per hectare) will generate a linear relationship self-thinning line of constant slope. Nevertheless, the suitability of these theoretical relationships for describing the self-thinning process has been challenged over the past three decades (Drew and Flewelling, 1977; Lonsdale, 1990; Zeide, 1987).

The self-thinning power law states that without disturbance, stand density decreases exponentially with increasing individual size (Yoda et al., 1963). Recently, the stand self-thinning theory was extended to understocked stands (Tang et al., 1994). The revised self-thinning theory assumes that self-thinning starts before a stand reaches maximum density, and the self-thinning rate increases with stand density and reaches a maximum at the maximum stem number (MSN).

2.2.2 Maximum stem number theory

Kira et al. (1953, 1954) developed the basic theory of C-D using agricultural plants;

$$\frac{1}{w_t} = a \cdot p + b \tag{1}$$

where, w_t is final yield of a plant at time t, p is the number of individuals per unit area, and a

and *b* are coefficients.

Tadaki (1963) expanded this approach to apply to forests, whereby height, representing the stage of biological development, was substituted for time. Thus, $1/V = a \cdot p + b$, where *V* is average volume per tree, *p* is number of trees per unit area, and *a* and *b* are functions of height. Goulding (1972) applied Kira's C-D rule to develop the *dbh* growth function (Eq. 2);

$$dbh = \frac{1}{a_0 \cdot ho^{a_1} \cdot SN + b_0 \cdot ho^{b_1}} \tag{2}$$

where, *ho* is the dominant tree height and *SN* is stand density. This was an excellent fit and the model was then tested for its ability to predict net growth (Goulding, 1972; Lee et al., 2000).

Based on equation 2, Sterba developed a theory stating that the stand density maintaining maximum basal area is the MSN (Sterba, 1987, 1975). First, basal area was estimated by multiply equation 2 by the stand density (Eq. 3).

$$BA = \pi \cdot \left(\frac{dbh}{200}\right)^2 \cdot SN = \frac{\pi}{40000} \cdot \left\{ \frac{SN}{\left(a_0 \cdot ho^{a_1} \cdot SN + b_0 \cdot ho^{b_1}\right)^2} \right\} \tag{3}$$

The stand density increased with the basal area, until the maximum value of the basal area was approached. Once the maximum value of the basal area is achieved, it will be very stable and experience few changes. Therefore, second, the MSN is the stand density that is approaching the maximum value of the basal area. In conclusion, the function of MSN was derived from the application of equation 3 to a differential equation, from which a value of zero was obtained (Eq. 4 and 5)

$$\frac{\delta BA}{\delta SN} = \frac{\pi}{40000} \cdot \left\{ \frac{b_0 \cdot ho^{b_1} - a_0 \cdot ho^{a_1} \cdot SN}{\left(a_0 \cdot ho^{a_1} \cdot SN + b_0 \cdot ho^{b_1}\right)^3} \right\} \tag{4}$$

$$MSN = \frac{b_0 \cdot ho^{b_1}}{a_0 \cdot ho^{a_1}} = \left(\frac{b_0}{a_0}\right) \cdot ho^{(b_1 - a_1)} \tag{5}$$

2.2.3 Self-thinning model

To reflect current principles of self-thinning, we applied Sterba’s theory, which is based on the competition density (C-D) effect and dominant tree height, to develop the self-thinning model of stand level in this study. We used observations of *ho*, *dbh* and *SN* to fit the parameters of the MSN. *ho* is one of the most commonly used indicators of site productivity because a close correlation exists between volume and site index, and it is generally accepted that the height of *ho* is minimally affected by competition.

In this study, the self-thinning model was designed with regard to the ratio of current stand density, MSN, and relative stand density. The following model for the self-thinning limit was estimated using the MSN curve:

$$\frac{SN_i - SN_{i+1}}{MSN_i - MSN_{i+1}} = a \cdot e^{b \frac{SN_i}{MSN_i}}, \quad \Delta SN_i = a \cdot e^{b \frac{SN_i}{MSN_i}} \cdot (MSN_i - MSN_{i+1}) \tag{6}$$

where, *i* is stand age (years), SN_i is stand density at time *i*, MSN_i is maximum stem number at time *I*, Δ*SN* is the number of dying trees from *i* to *i+1*, and a and *b* represent the self-thinning index.

Coefficient *a* is mortality when SN_i and MSN_i have the same value. Therefore, conceptually, it should be estimated as 1. Coefficient *b* is the self-thinning index and is generally considered a constant for a particular species such as the -3/2 self-thinning power law. Data used to estimate the stand-level mortality the next growth period, as a function of tree and stand characteristics, were obtained from the whole data set including all plots and measurements (Table 1).

2.3 Validation

The following four statistics, which can provide almost all of the information necessary for model validation (Burk, 1986; Cao, 2000), were used in this study to validate the developed mortality function for temperate forests

$$\text{Mean deviation} = \sum_{i=1}^{n} (Y_i - P_i)/n$$

$$\text{Mean absolute deviation} = \sum_{i=1}^{n} |Y_i - P_i|/n$$

$$\text{Standard deviation of difference} = \sqrt{\sum_{i=1}^{n} (D_i - \overline{D})^2/(n-1)}$$

$$\text{Root Mean Square Deviation (RMSD)} = \sqrt{\sum_{i=1}^{n} (Y_i - P_i)^2/n}$$

where, Y_i is the observed stand-level mortality of the *i*th plot, with 100 (%) being every tree died in a plot and 0 (%) being every tree survived in a plot; P_i is the predicted stand-level mortality of the *i*th plot; *n* is the total number of plots in data set of each tree species; D_i is the difference between Y_i and P_i and $\overline{D}$ is the average of the all difference. The overall mean deviation and overall mean absolute deviation were calculated based on all Korean NFI data. In addition to the four validation statistics, the observed number of dead trees was also compared to the predicted number of dead trees by 10-cm diameter classes and 4-m *ho* classes created above.

2.4 Residual analysis

Any spatial scales of climate present spatial patterns. Therefore, although the mortality model had a good statistical fit and random pattern of residuals, the residual can exhibit spatial autocorrelation if climate influences tree mortality.

Therefore, we checked the spatial autocorrelation of residuals, such as the difference between the observed value of the dependent variable (y) and the predicted value (ŷ). 'Spatial autocorrelation' is the correlation among values of a single variable strictly attributable to their relatively close locational positions on a two-dimensional (2-D) surface, introducing a deviation from the independent-observation assumption of classical statistics. Spatial autocorrelation exists because real-world phenomena are typified by orderliness, (map) pattern, and systematic concentration, rather than randomness.

If differences in residuals exist at the regional level as a result of other factors, such as climatic or topographic factors, the residuals will show spatial autocorrelation. We used the semi-variogram analysis to identify spatial autocorrelation (Bahn et al., 2008). In this paper, the semi-variograms used were all fitted to the spherical model (Vieira, 2000). We also estimated additional spatial parameters in residuals, in which spatial autocorrelation was included, using the SPATIAL STATS sub-module in the S-PLUS Program (Kirilenko and Solomon, 1998).

According to existing studies, tree mortality is associated with climatic water/heat stress (Kozlowski and Pallardy, 1997; Lambers et al., 2008). This shows that if residuals possess spatial autocorrelation, the relationship between tree mortality and climate factors can be analyzed quantitatively. Therefore, in the present study, we modeled the relationship between the seasonal mean temperature (2006–2013) and residuals using a simple linear function (Eq. 7):

$$e_i = a + b \cdot T_i \tag{7}$$

where, *i* is permanent plot number, *T* is the seasonal mean temperature during 2006–2013 at *i*, *a* and *b* is coefficient, and *e* is the residual of *i*.

3. Results and discussion

3.1 Maximum stem number (MSN) curve

All parameter estimates of the MSN curve are logical and significant at the 0.05 level (Table 2). The estimated MSN curves for each tree species using plot information from the NFI dataset and yield tables from the Korea Forest Service (2009) are shown in Figure 1 for comparison. The Korean yield tables include forest stand status (such as *dbh*, stand mean height, dominant tree height, stand density, and basal area) by each tree species in 5-year intervals, ranging from 15 to 80 years of age. The stand density in NFI permanent plots tended to decrease markedly as the height of dominant trees increased for each tree species in this study. This is because *ho* is related to stand age, light input to the ground, and resulted in tree mortality (Schwinning and Weiner, 1997).

The estimated MSN curve for every tree species passes through the maximum tree number over the dominant tree height using the observed data from NFI and yield tables. The upper part of the observed data from the NFI and yield tables could indicate the maximum tree number according to the dominant tree height in nature. Therefore, the estimated MSN curve could indicate that the model successfully reflected the trends for maximum tree number for Korean major forests according to dominant tree height at the national scale, although uncertainties remain for individual stand environments. In theory, the estimated MSN curve had the highest stand density among permanent sample plots at the same dominant tree height. However, some of the plots had higher stand density than the estimated MSN of each tree species due to special environmental conditions, observational error and others reasons. This is not an issue for the present study because such plots accounted for only 2.5% of the total sample plots, and our mortality model is applicable to any forest regardless of the present stand density.

Our results showed that the MSN of red pine, Japanese larch, Korean pine, Chinese cork oak, and Mongolian oak changed from 4,455, 8,319, 4,040, 5,456, and 4,102 trees per ha at the dominant tree height of 10 m to 818, 298, 161, 608, and 402 trees per ha at the dominant tree height of 30 m, respectively (Fig. 1f). This shows that the species with the highest and lowest MSN at the dominant tree height of 10 m were Japanese larch and red pine. In contrast, the species with the highest and lowest MSN at the dominant tree height of 30 m were Korean pine and red pine. Thus, Japanese larch and Korean pine had higher mortality (96%) than the other tree species, and red pine had the lowest mortality (82%) in the 10 to 30 m range of dominant tree height.

<Table 2>

<Figure 1>

3.2 Mortality model

Table 3 shows the parameter estimates and related statistics for the mortality model. For all species, the *SN*-to-*MSN* ratio was highly significant ($P < 0.001$) at predicting tree survival. These results indicate that there is close correlation between the *SN*-to-*MSN* ratio and mortality. The coefficient of the *SN*-to-*MSN* ratio is positive in all cases, resulting in an increase in mortality as the *SN*-to-*MSN* ratio increases. The stand-level mortality for all species decreased when the *SN*-to-*MSN* ratio decreased, thus, the mortality rate decreased as the space per tree in the stand increased.

When stand density was equal to MSN in the mortality model derived from this study, the change in stand density according to growth dominant tree height and the MSN curve over dominant tree height are the same. Therefore, coefficient *a* must theoretically be estimated at 1 in this mortality model. In this study, coefficient *a* in the mortality model of every tree species was estimated and rounded to 1 (Table 3). Consequently, the hypothesis about our mortality model match on the model results was confirmed.

Coefficient *b* of red pine, Japanese larch, Korean pine, Chinese cork oak, and Mongolian oak was estimated as 1.55, 1.38, 1.20, 1.18, and 0.98, respectively. Coefficient *b* reflects the effect of the *SN*-to-*MSN* ratio on mortality. Coefficient *b* of coniferous species (red pine, Japanese larch and Korean pine) was estimated to be high relative to that of oak species (Chinese cork oak and Mongolian oak). This result shows that the highest and the lowest mortality levels (Delta SN/stand density), according to a decrease in MSN of each stand in the 0 to 1 range on the *SN*-to-*MSN* ratio, were Mongolian oak and red pine. In contrast, red pine and Mongolian oak had the highest and lowest values in more than 1 range on the *SN*-to-*MSN* ratio. These results indicate that the mortality of oak species is relatively high compared to that of coniferous species until the density of each stand reaches MSN. In contrast, red pine and Mongolian oak have the highest and the lowest mortality at high stand densities ($SN > MSN$).

Figure 2 shows the measured and predicted delta SN for all plots in all measurements by tree species. The mean delta SN over 5-years for red pine, Japanese larch, Korean pine, Chinese cork oak, and Mongolian oak was 236.8, 252.0, 288.4, 314.6, and 163.6, respectively. The models showed relatively good performance when explaining variation in delta SN during the 5 years, with R^2 values ranging from 0.58 to 0.83. The R^2 of red pine, Japanese larch, Korean pine, Chinese cork oak, and Mongolian oak was estimated as 0.58, 0.72, 0.65, 0.62, and 0.83, respectively.

The results of the mortality model in Figure 2 exhibited uneven spreading of residuals. However, the result did not affect the level of statistical significance. From the original data set, the average of predicted and observed delta SN for red pine were 256.2 and 236.9, respectively, representing a mean deviation of -0.439 (Table 4). The corresponding delta SN were 298.1 and 252.0 (mean deviation -0.570) for Japanese larch, 272.3 and 288.4 (mean deviation 0.451) for Korean pine, 333.3 and 314.6 (mean deviation -0.152) for Chinese cork oak, and 140.1 and 163.6 (mean deviation 0.346) for Mongolian oak. The Chi-squared test provided no evidence of a lack of fit between the predicted and observed values for any of the tree species. Therefore, one possible interpretation for such results could be attributed to South Korea forest's uneven age-class distribution, in which trees that are less than 40 years comprise over 70% of South Korean forests (Kim et al., 2016).

The observed mortality in each stand followed a similar pattern but were slightly higher than that reported in previous studies (Shin et al., 2003). The mortality of red pine, Japanese larch, and Korean pine was estimated to be 4.6, 4.7, and 5.2% from previous studies that only considered four provinces of South Korea; however, the present study included an entire forest from the NFI dataset. In this context, the approach taken in the present study differs from that of previous studies, which used data of partial regions by successfully reflecting the changes in stand density.

Predicted and observed delta SN with respect to *dbh* are examined in Fig. 3. Generally, the predictions were close to the observed delta SN for all but the smallest *dbh* class (*dbh* < 10 cm). This result is similar to that shown in previous studies (Monserud and Sterba, 1999; Yang et al., 2003). When the number of trees in a stand is very small, they are susceptible to various mortality agents such as severe weather conditions and competing vegetation. Therefore, mortality rates at this stage are high and range widely. It is difficult to estimate the mortality of young or small trees for this reason, and the uncertainty of the results obtained from the model is higher than for stands of large trees.

Statistical fit is very important for determining whether a growth model is ‘good’ enough. However, it is even more important to evaluate a model’s ecological performances over a wide range of stand conditions. Compared with the automatic selection of predictor variables using a statistical method, fitting a growth model based on ecologically important variables is a better approach. It is recommended that this approach is adopted whenever possible, even at the expense of superior statistical properties in some cases. If a model is ecologically illogical, it will not perform well for any data set other than that used for model development (Hamilton, 1986). This approach was adopted in the present study to develop the self-thinning function for stand level of major temperate tree species in South Korea. The following predictor variables were present in the new mortality function: dominant tree height and stand density. The newly developed function out-performs the old function based on both model fitting and model validation results. All estimated coefficients were consistent with ecological expectations.

<Table 3>

<Figure 2>

3.3 Validation

Table 4 shows the overall mean deviation, the overall mean absolute deviation, and standard deviation of difference and RMSD by tree species between the observed and the predicted mortality. The mean deviations of red pine, Korean pine, and Mongolian oak were negative, indicating a tendency of overestimating survival. Conversely, the mean deviation for Korean pine and Chinese cork oak was estimated as positive. However, these deviations were all very small in magnitude and the over- and underestimation can be ignored. The statistical performance of other validation methods for every tree species remained significant. (Table 4). Therefore, we confirm that the mortality function performs well based on both model fitting and model validation results.

Tang et al. (1994) developed a mortality model that could be used in fully stocked or understocked stands. The model was applied using a variable self-thinning rate. Tang et al. (1994) assumed that the self-thinning rate of an understocked stand increases with stand density index until it becomes a fully-stocked stand. In this paper, we considered that the *SN-to-MSN* ratio of each stand is the self-thinning rate. These attempts have been verified to be useful to estimate the mortality and stand density at any given stand age with any initial stand conditions through statistical verification.

Fig. 3 shows the observed and predicted number of surviving trees by diameter class. For each diameter class, the number of dead trees predicted by the mortality model was close to the observed number. The same conclusion holds when dominant tree height is used for grouping the number of surviving trees (Fig. 4).

Crown-related variables, such as crown width or crown ratio (the ratio of live crown length to total tree height), have been commonly used to model tree growth and mortality (Monserud and Sterba, 1999; Wykoff et al., 1982). Those variables are good indicators of tree vigor and are preferred whenever possible. Unfortunately, those variables were not measured in the Korea NFI in the data set used and, therefore, could not be used here. However, as suggested by Monserud and Sterba (1999), one indicator of tree vigor might be sufficient for mortality modeling. Since increments in dominant tree height were already considered, the lack of crown-related variables was not viewed as problematic for the purpose of mortality modeling.

Similar to many mortality functions (e.g., Keister and Tidwell, 1975; Monserud, 1976), multiple predictor variables were used in this study, which are variables related to tree size, stand density, tree growth rate, and competition. Similar to several other mortality models (e.g., Campbell et al., 1979; Guan and Gertner, 1991), the developed mortality function is a deterministic and empirical function.

<Table 4>

<Figure 3>

<Figure 4>

3.4 Residual analysis

The spatial autocorrelation of residuals from the mortality model for each tree species is shown in the semi-variograms (Fig. 5). The range of semi-variogram values of red pine, Japanese larch, and Korean pine from the mortality model residuals was estimated as 29.2, 14.2, and 14.1 km, respectively. The partial sill values of these species were estimated as 8.9, 12.3, and 21.1, respectively. Conversely, sill values were not shown for oak species. This indicated that a very low degree of spatial autocorrelation is found in the mortality model residuals. These results suggested that coniferous species may vary in their level of mortality due to other factors with spatial autocorrelation in the range 14 to 30 km. Forests in South Korea cover a total area of 60,100 km^2 and have a complicated topography. Therefore, this spatial autocorrelation may be associated with climatic rather than topographic factors.

Seasonal correlations between temperature and residual in Figure 6A have significant positive relationships in every season for coniferous species except Korean pine during winter months. In contrast, the correlations found in oak species show a weak negative correlation in every season except cork oak during winter. Spring temperature is the highest correlated variable with the residuals of Japanese larch, Korean pine and cork oak. For other species, winter temperature had the highest correlation coefficient. Correlation analysis results indicate the optimal seasonal temperature for maximum circumference growth of each tree species which was determined by selecting the highest correlation coefficient among seasonal temperatures for a given species. Table 5 illustrates the significance level of coefficients determined by the regression analysis, which examines the relationship between the mortality model residuals and optimal seasonal temperature between 2006 and 2013.

The regression analysis showed relatively good statistical performance in terms of the significance level of coefficients in coniferous species and bad statistical performance for the oak species. The results obtained by the regression analysis are similar to those of the variogram analysis. In other words, these results reveal that the mortality of coniferous species has been strongly affected by temperature, while the mortality of oaks has not. This can be seen more clearly in Fig. 6b. The effects of the optimal seasonal temperature on mortality are visualized.

The mortality model residuals of coniferous species tended to increase when the seasonal mean temperature increased (Fig. 6b). The coefficient of determination (R^2) suggested that approximately 6.0–13.0% of mortality variability could be explained by annual average temperature for coniferous trees. The regression model of each coniferous tree had a low R^2

value, they showed relatively good statistical performance in terms of the significance level of coefficients (Table 5). This means that temperature is one of the aggravating drivers of coniferous mortality in South Korea’s forests.

Some of major climatic variables, such as the hydrological component, were excluded from the analysis and this has certain limitations; however, the effects of temperature on each species were confirmed through the study. According to the regression analysis, the observed mortality was higher than the predicted mortality for red pine, Japanese larch and Korean pine forest area. This indicates that the rising temperature accounts for the observed mortality area for each species that covers 57.8, 61.4, and 76.6%, respectively.

This reveals that temperature is a potent driver of coniferous forest tree mortality and is accelerating tree death in almost coniferous forest in South Korea. This result is not only similar to findings of previous studies in South Korean forests (Byun et al., 2013; Lee et al., 2008), but also of studies worldwide (Dobbertin et al., 2005; Landmann et al., 2006; Martinez-Vilalta and Piñol, 2002; van Mantgem and Stephenson, 2007). Conversely, the mortality rates of the oaks tended to nonsignificantly decrease with increasing temperature.

The common causal factors in these examples are elevated temperatures and/or water stress, raising the possibility that the world’s forests are increasingly responding to ongoing warming and dying. Although a range of responses can and should be expected, recent cases of increased tree mortality and die-offs triggered by drought and/or high temperatures raise the possibility that amplified forest mortality may already be occurring in some locations in response to global climate change. Allen et al. (2010) presented a global assessment of recent tree mortality attributed to drought and heat stress.

The present findings are consistent with those of previous studies. Byun et al. (2013) reported that in ranges of ~40 km, standardized radial growth of red pine showed spatial autocorrelation by climate factors. In addition, it has also been reported that the temperature increment has a negative effect on the growth of red pine. This is attributed to the fact that high temperatures induce water stress that would limit radial growth in red pine. Furthermore, in other many studies, incremental temperature had negative impacts on forest growth and on the distribution of red pine, Japanese larch, and Korean pine in South Korean forests (Choi et al., 2015; Nam et al., 2015; Byun et al. 2013).

In general, the concomitant increase in morality and decline in diameter increment by temperatures rise is a paradoxical phenomenon in natural forest. In addition, this phenomenon suggests that coniferous forests in South Korea could be more sensitive to increases in temperature than oak forests. These results suggest that coniferous forests could be increasingly vulnerable to climate- and associated infestation-induced tree-mortality events. Extensive tree mortality (‘forest die-off’) triggered by dry and hot climatic conditions has been documented on every vegetated continent and in most bioregions over the past two decades (Allen et al., 2010; Kurz et al., 2008; van Mantgem et al., 2009). Many recent examples of drought and heat-related tree mortality from around the world suggest that no forest type or climate zone is invulnerable to anthropogenic climate change, even in environments not normally considered water-limited.

Precipitation variables are not factored into this research. The main reason for the decision is based on the current status and the future scenarios of climate changes in South Korea. In most of scientific studies on the future climate of South Korea, temperature was predicted to significantly increase whereas a slight increment was projected for precipitation (Lee et al., 2014; Lee et al., 2013). Therefore, temperature will probably function more as a limiting factor for facilitating mortality than precipitation. However, we acknowledge the necessity to consider hydrological variables such as stress moisture/heat index in future studies for improving the result of model suitability.

There are major scientific uncertainties in our understanding of climate-induced tree mortality, particularly regarding the mechanisms that drive mortality, including physiological thresholds of tree death and interactions with biotic agents. Recent advances in the understanding of tree mortality mechanisms suggest that forests could be particularly sensitive to increases in temperature in addition to drought alone, especially in cases where carbon starvation rather than hydraulic failure is the primary mechanism of tree mortality. However, we currently lack the ability to predict mortality and die-off of tree species and forest types based on specific combinations of climatic events and their interactions with biotic stressors and place-specific site conditions.

<Table 5>

<Figure 5>

<Figure 6>

4. Conclusion

From the estimated MSN curve, it could be inferred that the model successfully reflected the trend of maximum tree number observed for Korean major forests according to dominant tree height at the national scale while uncertainties remain for individual stand environments. In addition, the present study showed that the *SN*-to-*MSN* ratio in each stand is closely linked to tree morality in forest stands and has potential for use as a new index, such as Reineke’s Stand

Density Index. The self-thinning model accurately described the *SN*-to-*MSN* ratio-mortality relationship of every tree species with different initial stand density and different site quality.

Our results showed that increased tree mortality in Korean coniferous forests is associated with warmer conditions. However, the response of tree mortality differs among species as can be seen in the case of oak species, in which rising temperature tends to have a positive effect, although its level of significance has not been obtained. This in part indicates that coniferous species could be more sensitive than oak species to climate change in South Korea. Despite the findings of this study, the complexity and scientific uncertainties of climate-induced tree mortality challenge our understanding, particularly regarding the mechanisms that drive mortality including physiological thresholds of tree death and interactions with biotic agents. Therefore, further studies that explain the interactions with tree mortality and climate will offer a useful way to disclose areas of scientific uncertainties and will provide a meaningful representation for forest management practices and policies.

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