

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

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21 **Abstract**

22 Mortality is a key process in forest stand dynamics. However, tree mortality is not well  
23 understood, particularly in relation to climatic factors. The objectives of this study were to: (i)  
24 determine the patterns of maximum stem number per ha (MSN) over dominant tree height from  
25 5-year remeasurements of the permanent sample plots for temperate forests [Red pine (*Pinus*  
26 *densiflora*), Japanese larch (*Larix kaempferi*), Korean pine (*Pinus koraiensis*), Chinese cork  
27 oak (*Quercus variabilis*), and Mongolian oak (*Quercus mongolica*)] using Sterba's theory and  
28 Korean National Forest Inventory (NFI) data, (ii) develop a stand-level mortality (self-thinning)  
29 model using the MSN curve, and (iii) assess the impact of temperature on tree mortality in  
30 semi-variogram and linear regression models. The MSN curve represents the upper boundary  
31 of observed stem numbers per ha. The developed mortality model with our results showed a  
32 high degree of reliability ( $R^2 = 0.55-0.81$ ) and no obvious dependencies or patterns in residuals.  
33 However, spatial autocorrelation was detected from residuals of coniferous species (Red pine,  
34 Japanese larch and Korean pine), but not for oak species (Chinese cork oak and Mongolian  
35 oak). Based on the linear regression analysis of residuals, we found that the mortality of  
36 coniferous forests tended to increase with the rising seasonal temperature. This is more evident  
37 during winter and spring months. Conversely, oak mortality did not significantly vary with  
38 increasing temperature. These findings indicate that enhanced tree mortality due to rising  
39 temperatures in response to climate change is possible, especially in coniferous forests, and is  
40 expected to contribute to forest management decisions.

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

43

## 44 **1. Introduction**

45 Tree mortality is key process in stand dynamics and a highly complicated process. It is affected  
46 by a variety of environmental, physiological, pathological, and entomological factors, as well  
47 as random events. Generally, tree death results from complex interactions among multiple  
48 factors and is often a gradual process, although it can sometimes be abrupt (Waring, 1987).  
49 Some factors weaken trees, while others directly cause tree death (Manion, 1981). Due to the  
50 complexity of the mortality process and uncertainty in the timing of tree death, mortality  
51 remains one of the least understood components of growth and yield estimation (Hamilton,  
52 1990).

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

64 The mortality models have also generally been classified as two groups, tree- and stand-level  
65 models (Landsberg and Sands, 2011). Tree-level models had relatively complex algorithms and  
66 more uses for modeling the dynamics of uneven-sized stands than stand-level models (Groot  
67 et al., 2004; Vanclay, 1994). Stand-level models have helped to forecast of forest resource

68 conditions, as growth and yield in terms of volume, changes in order to obtain relevant  
69 information for sound decision making (Landsberg and Sands, 2011).

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

79 Tree mortality is a natural ecological process (Franklin et al., 1987); however, drought- and  
80 heat-induced mortality, including associated infestation-related forest die-off, is often a  
81 selective force that differentially affects tree species and rapidly alters the size, age, and spatial  
82 structure of forests. Growing evidence suggests that many forests could be increasingly  
83 vulnerable to climate- and infestation-induced tree-mortality events (Allen et al., 2010; Hember  
84 et al., 2016). The significant interaction between climate and tree mortality for 11 common  
85 species, mainly pine and oak species, in Mediterranean regions was reported (Ruiz-Benito et  
86 al., 2013). Increased mortality are also associated with climate condition among many  
87 temperate tree species pine and fir species in central Turkey (Semerci et al., 2008), *Pinus*  
88 *tabulaeformis* in east-central China (Wang et al., 2007), *Abies koreana* in South Korea (Lim et  
89 al., 2008). Investigation into the physiological mechanisms through which dry and hot climatic  
90 conditions drive tree death and forest die-off represent a rapidly growing research area  
91 (McDowell et al., 2008; Sala et al., 2010), but the impact of forest die-off remains less well

92 studied. Climate-induced forest mortality seems to be an emerging global phenomenon, yet  
93 there is very rare synthesis of the ecological, societal, and climatological consequences of dying  
94 forests at present.

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

101

## 102 **2. Materials and methods**

### 103 **2.1 Description of South Korea forest and National Forest Inventory**

104 South Korea forests occupy ~64% (6,450,438 ha) of total land area in the country. Evergreen  
105 needleleaf (mainly *Pinus densiflora*), deciduous broadleaf (mainly *Quercus* spp.), and mixed  
106 forests took up approximately 40.5%, 27%, and 29.3% of total forest area in 2015, respectively.  
107 South Korea's forest have been intensively managed and stocking volume has increased from  
108 8.2 m<sup>3</sup> ha<sup>-1</sup> in 1954 to 142.2 m<sup>3</sup> ha<sup>-1</sup> in 2014 (Korea Forest Service, 2015). Currently, 69.5%  
109 of South Korean forests are less than 40 years old.

110 We used remeasurements from permanent plots of the Korean NFI for mortality and survival  
111 data (Korea Forest Service, 2015). A systematic 4-km grid of permanent plots covering South  
112 Korea was established in 2006–2010 (Korea Forest Research Institute, 2011). Each year, 20%  
113 of grid locations were sampled in a manner that the whole of South Korea was covered by the  
114 inventory each year. Each location was then remeasured from 2011–2015, exactly 5 years after  
115 the establishment. The total inventory comprises 4,200 clusters, consisting of 16,800  
116 permanent plots. Four circular sample plots were located at the intersection of each 4 × 4-km

117 grid line. Each sample plot (31.6-m radius) covered 0.16 ha. Forest characteristics (tree species,  
118 age, and height), diameter at breast height (*dbh*), number of trees with a diameter greater than  
119 6 cm, and topographical factors (coordinates, elevation, slope, and aspect) were measured at  
120 all sites. Tree species identification of plots was determined according to basal area of the  
121 dominant species. If basal area of red pine occupied more than 75% in a plot, the plot was  
122 considered a "red pine" stand.

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

131 In this study, we used the Korean NFI remeasured data and evaluated the status of more than  
132 1,484 permanent plots of the five main temperate tree species in South Korea (Table 1), which  
133 include red pine (*Pinus densiflora*), Japanese larch (*Larix kaempferi*), Korean pine (*Pinus*  
134 *koraiensis*), Chinese cork oak (*Quercus variabilis*), and Mongolian oak (*Quercus mongolica*).  
135 These tree species form large forests in most of the mountainous areas of South Korea,  
136 occupying approximately 37%, 5%, 4%, 5%, and 11%, respectively, of the total forested area  
137 in 2010. Based on a sample of 1,484 permanent plots, the overall 5-year mortality rate is 16.2%,  
138 which corresponds to an annual rate of 3.2% yr<sup>-1</sup> (Table 1). The most common species, red  
139 pine, has an annual mortality rate of 2.8% yr<sup>-1</sup>. Annual mortality rates for other coniferous  
140 species vary between 5.2% yr<sup>-1</sup> for Korean pine and 5.1% yr<sup>-1</sup> for Japanese larch. Chinese cork  
141 oak and Mongolian oak were 4.2% yr<sup>-1</sup> and 2.2% yr<sup>-1</sup>.

142

143 <Table 1>

144

## 145 **2.2 Stand-level mortality model**

### 146 **2.2.1 Background of self-thinning principles**

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

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

159

### 160 **2.2.2 Maximum stem number theory**

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

$$162 \frac{I}{w_t} = a \cdot p + b \tag{1}$$

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

164 and  $b$  are coefficients.

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

169

$$170 \quad dbh = \frac{I}{a_0 \cdot ho^{a_1} \cdot SN + b_0 \cdot ho^{b_1}} \quad (2)$$

171

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

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

177

$$178 \quad BA = \pi \cdot \left( \frac{dbh}{200} \right)^2 \cdot SN = \frac{\pi}{40000} \cdot \left\{ \frac{SN}{\left( a_0 \cdot ho^{a_1} \cdot SN + b_0 \cdot ho^{b_1} \right)^2} \right\} \quad (3)$$

179

180 The stand density increased with the basal area, until the maximum value of the basal area was  
181 approached. Once the maximum value of the basal area is achieved, it will be very stable and  
182 experience few changes. Therefore, second, the MSN is the stand density that is approaching  
183 the maximum value of the basal area. In conclusion, the function of MSN was derived from



184 the application of equation 3 to a differential equation, from which a value of zero was obtained  
 185 (Eq. 4 and 5)

186

$$187 \quad \frac{\delta BA}{\delta SN} = \frac{\pi}{40000} \cdot \left\{ \frac{b_0 \cdot ho^{b_1} - a_0 \cdot ho^{a_1} \cdot SN}{(a_0 \cdot ho^{a_1} \cdot SN + b_0 \cdot ho^{b_1})^3} \right\} \quad (4)$$

$$188 \quad MSN = \frac{b_0 \cdot ho^{b_1}}{a_0 \cdot ho^{a_1}} = \left( \frac{b_0}{a_0} \right) \cdot ho^{(b_1 - a_1)} \quad (5)$$

189

### 190 **2.2.3 Self-thinning model**

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

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

200

$$201 \quad \frac{SN_i - SN_{i+1}}{MSN_i - MSN_{i+1}} = a \cdot e^{\frac{b \cdot SN_i}{MSN_i}}, \quad \Delta SN_i = a \cdot e^{\frac{b \cdot SN_i}{MSN_i}} \cdot (MSN_i - MSN_{i+1}) \quad (6)$$

202

203 where, *i* is stand age (years), *SN<sub>i</sub>* is stand density at time *i*, *MSN<sub>i</sub>* is maximum stem number at

204 time  $I$ ,  $\Delta SN$  is the number of dying trees from  $i$  to  $i+I$ , and  $a$  and  $b$  represent the self-thinning  
205 index.

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

211

### 212 **2.3 Validation**

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

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

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

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

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

220 where,  $Y_i$  is the observed stand-level mortality of the  $i$ th plot, with 100 (%) being every tree  
221 died in a plot and 0 (%) being every tree survived in a plot;  $P_i$  is the predicted stand-level  
222 mortality of the  $i$ th plot;  $n$  is the total number of plots in data set of each tree species;  $D_i$  is the

223 difference between  $Y_i$  and  $P_i$  and  $\bar{D}$  is the average of the all difference. The overall mean  
224 deviation and overall mean absolute deviation were calculated based on all Korean NFI data.  
225 In addition to the four validation statistics, the observed number of dead trees was also  
226 compared to the predicted number of dead trees by 10-cm diameter classes and 4-m *ho* classes  
227 created above.

228

## 229 **2.4 Residual analysis**

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

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

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

246 According to existing studies, tree mortality is associated with climatic water/heat stress  
247 (Kozłowski and Pallardy, 1997; Lambers et al., 2008). This shows that if residuals possess  
248 spatial autocorrelation, the relationship between tree mortality and climate factors can be  
249 analyzed quantitatively. Therefore, in the present study, we modeled the relationship between  
250 the seasonal mean temperature (2006–2013) and residuals using a simple linear function (Eq.  
251 7):

252

$$253 \quad e_i = a + b \cdot T_i \quad (7)$$

254

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

257

### 258 **3. Results and discussion**

#### 259 **3.1 Maximum stem number (MSN) curve**

260 All parameter estimates of the MSN curve are logical and significant at the 0.05 level (Table  
261 2). The estimated MSN curves for each tree species using plot information from the NFI dataset  
262 and yield tables from the Korea Forest Service (2009) are shown in Figure 1 for comparison.  
263 The Korean yield tables include forest stand status (such as  $dbh$ , stand mean height, dominant  
264 tree height, stand density, and basal area) by each tree species in 5-year intervals, ranging from  
265 15 to 80 years of age. The stand density in NFI permanent plots tended to decrease markedly  
266 as the height of dominant trees increased for each tree species in this study. This is because  $ho$   
267 is related to stand age, light input to the ground, and resulted in tree mortality (Schwinning and  
268 Weiner, 1997).

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

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

291

292 <Table 2>

293 <Figure 1>

294

### 295 **3.2 Mortality model**

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

303 When stand density was equal to MSN in the mortality model derived from this study, the  
304 change in stand density according to growth dominant tree height and the MSN curve over  
305 dominant tree height are the same. Therefore, coefficient  $a$  must theoretically be estimated at  
306 1 in this mortality model. In this study, coefficient  $a$  in the mortality model of every tree species  
307 was estimated and rounded to 1 (Table 3). Consequently, the hypothesis about our mortality  
308 model match on the model results was confirmed.

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

318 coniferous species until the density of each stand reaches MSN. In contrast, red pine and  
319 Mongolian oak have the highest and the lowest mortality at high stand densities ( $SN > MSN$ ).  
320 Figure 2 shows the measured and predicted delta SN for all plots in all measurements by tree  
321 species. The mean delta SN over 5-years for red pine, Japanese larch, Korean pine, Chinese  
322 cork oak, and Mongolian oak was 236.8, 252.0, 288.4, 314.6, and 163.6, respectively. The  
323 models showed relatively good performance when explaining variation in delta SN during the  
324 5 years, with  $R^2$  values ranging from 0.58 to 0.83. The  $R^2$  of red pine, Japanese larch, Korean  
325 pine, Chinese cork oak, and Mongolian oak was estimated as 0.58, 0.72, 0.65, 0.62, and 0.83,  
326 respectively.

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

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

343 of previous studies, which used data of partial regions by successfully reflecting the changes  
344 in stand density.

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

353 Statistical fit is very important for determining whether a growth model is ‘good’ enough.  
354 However, it is even more important to evaluate a model’s ecological performances over a wide  
355 range of stand conditions. Compared with the automatic selection of predictor variables using  
356 a statistical method, fitting a growth model based on ecologically important variables is a better  
357 approach. It is recommended that this approach is adopted whenever possible, even at the  
358 expense of superior statistical properties in some cases. If a model is ecologically illogical, it  
359 will not perform well for any data set other than that used for model development (Hamilton,  
360 1986). This approach was adopted in the present study to develop the self-thinning function for  
361 stand level of major temperate tree species in South Korea. The following predictor variables  
362 were present in the new mortality function: dominant tree height and stand density. The newly  
363 developed function out-performs the old function based on both model fitting and model  
364 validation results. All estimated coefficients were consistent with ecological expectations.

365 <Table 3>

366 <Figure 2>



367

### 368 **3.3 Validation**

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

378 Tang et al. (1994) developed a mortality model that could be used in fully stocked or  
379 understocked stands. The model was applied using a variable self-thinning rate. Tang et al.  
380 (1994) assumed that the self-thinning rate of an understocked stand increases with stand density  
381 index until it becomes a fully-stocked stand. In this paper, we considered that the *SN-to-MSN*  
382 ratio of each stand is the self-thinning rate. These attempts have been verified to be useful to  
383 estimate the mortality and stand density at any given stand age with any initial stand conditions  
384 through statistical verification.

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

389 Crown-related variables, such as crown width or crown ratio (the ratio of live crown length to  
390 total tree height), have been commonly used to model tree growth and mortality (Monserud

391 and Sterba, 1999; Wykoff et al., 1982). Those variables are good indicators of tree vigor and  
392 are preferred whenever possible. Unfortunately, those variables were not measured in the Korea  
393 NFI in the data set used and, therefore, could not be used here. However, as suggested by  
394 Monserud and Sterba (1999), one indicator of tree vigor might be sufficient for mortality  
395 modeling. Since increments in dominant tree height were already considered, the lack of  
396 crown-related variables was not viewed as problematic for the purpose of mortality modeling.  
397 Similar to many mortality functions (e.g., Keister and Tidwell, 1975; Monserud, 1976),  
398 multiple predictor variables were used in this study, which are variables related to tree size,  
399 stand density, tree growth rate, and competition. Similar to several other mortality models (e.g.,  
400 Campbell et al., 1979; Guan and Gertner, 1991), the developed mortality function is a  
401 deterministic and empirical function.

402

403 <Table 4>

404 <Figure 3>

405 <Figure 4>

406

### 407 **3.4 Residual analysis**

408 The spatial autocorrelation of residuals from the mortality model for each tree species is shown  
409 in the semi-variograms (Fig. 5). The range of semi-variogram values of red pine, Japanese larch,  
410 and Korean pine from the mortality model residuals was estimated as 29.2, 14.2, and 14.1 km,  
411 respectively. The partial sill values of these species were estimated as 8.9, 12.3, and 21.1,  
412 respectively. Conversely, sill values were not shown for oak species. This indicated that a very  
413 low degree of spatial autocorrelation is found in the mortality model residuals. These results  
414 suggested that coniferous species may vary in their level of mortality due to other factors with

415 spatial autocorrelation in the range 14 to 30 km. Forests in South Korea cover a total area of  
416 60,100 km<sup>2</sup> and have a complicated topography. Therefore, this spatial autocorrelation may be  
417 associated with climatic rather than topographic factors.

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

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

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

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

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

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

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

461 The present findings are consistent with those of previous studies. Byun et al. (2013) reported  
462 that in ranges of ~40 km, standardized radial growth of red pine showed spatial autocorrelation

463 by climate factors. In addition, it has also been reported that the temperature increment has a  
464 negative effect on the growth of red pine. This is attributed to the fact that high temperatures  
465 induce water stress that would limit radial growth in red pine. Furthermore, in other many  
466 studies, incremental temperature had negative impacts on forest growth and on the distribution  
467 of red pine, Japanese larch, and Korean pine in South Korean forests (Choi et al., 2015; Nam  
468 et al., 2015; Byun et al. 2013).

469 In general, the concomitant increase in mortality and decline in diameter increment by  
470 temperatures rise is a paradoxical phenomenon in natural forest. In addition, this phenomenon  
471 suggests that coniferous forests in South Korea could be more sensitive to increases in  
472 temperature than oak forests. These results suggest that coniferous forests could be increasingly  
473 vulnerable to climate- and associated infestation-induced tree-mortality events. Extensive tree  
474 mortality ('forest die-off') triggered by dry and hot climatic conditions has been documented  
475 on every vegetated continent and in most bioregions over the past two decades (Allen et al.,  
476 2010; Kurz et al., 2008; van Mantgem et al., 2009). Many recent examples of drought and heat-  
477 related tree mortality from around the world suggest that no forest type or climate zone is  
478 invulnerable to anthropogenic climate change, even in environments not normally considered  
479 water-limited.

480 Precipitation variables are not factored into this research. The main reason for the decision is  
481 based on the current status and the future scenarios of climate changes in South Korea. In most  
482 of scientific studies on the future climate of South Korea, temperature was predicted to  
483 significantly increase whereas a slight increment was projected for precipitation (Lee et al.,  
484 2014; Lee et al., 2013). Therefore, temperature will probably function more as a limiting factor  
485 for facilitating mortality than precipitation. However, we acknowledge the necessity to

486 consider hydrological variables such as stress moisture/heat index in future studies for  
487 improving the result of model suitability.

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

497

498 <Table 5>

499 <Figure 5>

500 <Figure 6>

501

#### 502 **4. Conclusion**

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

508 Density Index. The self-thinning model accurately described the *SN-to-MSN* ratio-mortality  
509 relationship of every tree species with different initial stand density and different site quality.  
510 Our results showed that increased tree mortality in Korean coniferous forests is associated with  
511 warmer conditions. However, the response of tree mortality differs among species as can be  
512 seen in the case of oak species, in which rising temperature tends to have a positive effect,  
513 although its level of significance has not been obtained. This in part indicates that coniferous  
514 species could be more sensitive than oak species to climate change in South Korea. Despite the  
515 findings of this study, the complexity and scientific uncertainties of climate-induced tree  
516 mortality challenge our understanding, particularly regarding the mechanisms that drive  
517 mortality including physiological thresholds of tree death and interactions with biotic agents.  
518 Therefore, further studies that explain the interactions with tree mortality and climate will offer  
519 a useful way to disclose areas of scientific uncertainties and will provide a meaningful  
520 representation for forest management practices and policies.

521

## 522 **Acknowledgement**

523 Special thanks to the Korea Forest Service and Korea Forest Inventory Center for providing  
524 the National Forest Inventory data set. This area of research is supported by the Korea Ministry  
525 of Environment under the “Climate Change Correspondence Program” (Project Number:  
526 2014001310008).

527

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