Quantifying height growth and monthly growing degree days relationship of plantation Taiwan spruce

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A B S T R A C T

The future of the endemic Taiwan spruce (Picea morrisonicola) under climate change is of great concern. It is the southernmost species of the genus and its current distribution is limited to high altitudes of Taiwan. As a first step toward assessing the impact of future temperature changes on the species, we quantified the effects of past monthly growing degree days (GDD) on the height growth of plantation Taiwan spruce based on nonlinear mixed-effects growth analysis. Our results showed that past GDD variations had both positive and negative effects on the height growth of the species. July of the preceding year had the greatest influence on current year height growth. An increase in the mean GDD level of the current May would also promote height growth. In contrast, a warmer previous November or current January had negative effects on height growth. If the established height growth–GDD relationship holds, the influences of climate change on Taiwan spruce height growth will depend on the timing of the temperature increases, as well as on the trees current growth stages. Our results suggested that a warmer climate would have a greater influence on trees that are still in the early stages along the height growth trajectory. The established height growth–GDD relationship will be a keystone for developing models assessing how Taiwan spruce responds to climate change.

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1. Introduction

Recent studies on growth–climate relationships of tree populations located at their species’ geographical distribution limits have proven to be valuable in assessing climate change impact (e.g., Mäkinen et al., 2000; Gamache and Payette, 2004; Wilmking et al., 2004; Andreu et al., 2007). Growth–climate relationships for species exhibiting a limited distribution at both a local and a global scale have attracted less attention. However, because such species typically possess a narrow climatic envelope, they are likely to be the most vulnerable to climate change (Thomas et al., 2004). Taiwan is unique in that it is situated in a subtropical region, but has many endemic coniferous species at high altitudes. Thus, it provides an opportunity to address the effects of climate change on narrow endemics.

Among the conifers endemic to Taiwan, the future of Taiwan spruce (Picea morrisonicola Hay.) is of particular concern. It is the southernmost species of the genus (The Gymnosperm Database, http://www.conifers.org/pi/pic/index.htm, accessed on October 21, 2008) and is therefore important biogeographically. Although the species once had a broader geographic range (Tsukada, 1966), its current narrow distribution at high altitudes (Taiwan Forestry Bureau, 1995; Fig. 1) may reflect past environmental impacts leading to population decline. With the projected island-wide temperature likely to increase between 0.9 and 2.7 °C when the CO2 concentration doubles that of the 1961–1990 level (Hsu and Chen, 2002), the species may be at even greater risk for threats associated with future climate change. As an important component of Taiwan's subalpine forests, major changes in the species distribution will have a significant impact on the subalpine forest ecosystems of Taiwan.

In assessing the likely impact of climate change on tree species, explicitly quantifying tree growth–climate relationships is essential (Peterson et al., 2002). The main objective of this study was to quantify the effects of monthly growing degree days (GDD, C-day) on the height growth of Taiwan spruce, as height growth is closely linked to reproductive potential (e.g., Gamache and Payette, 2004). Several studies have also suggested that height growth should be more suitable than radial growth for examining the effects of climatic variations on tree growth (Jalkanen and Tuovinen, 2001; Pensa et al., 2005; but see Mäkinen, 1998). As an integrated measure of temperature effects, GDD is closely related to plant growth and development (Poethig, 2003; Trudgill et al., 2005).
2. Materials and methods

2.1. Study site and the species

This study was conducted in the Ta-Ta-Chia area of central Taiwan (23° 8' 29" N, 120° 8' 53" E, ca. 2500–2800 m a.s.l.; Fig. 1). The study site is just north of the Tropic of Cancer and within the transition zone between montane and subalpine rain forest biomes. Although Taiwan spruce is found at altitudes between 2300 and 3000 m throughout the mountain regions of Taiwan, it forms a large area of natural pure stand only in the study area.

The nearest weather station situated at a similar elevation is Alishan Weather Station (23° 30' N, 120° 48' E, 2,413 m a.s.l.) of Taiwan Central Weather Bureau. It is about 8 km west of the study site. Between 1954 and 2003, the mean annual temperature at the station was 10.7 °C (Fig. 2a). The mean annual precipitation at the station was approximately 3800 mm, which was characterized as a wet summer and dry winter (Fig. 2b).

As a species with only one annual flush, the complete height growth process of Taiwan spruce, from the beginning of terminal bud formation to the end of shoot elongation, is a 2-year process (Yong et al., 1998), which is similar to that of other conifers (e.g., Junttila, 1986). At the study site, Taiwan spruce winter terminal buds form during the current growing season and are visible in late August. Main shoot elongation usually begins in mid-May and completes in mid-June of the following year (Yong et al., 1998).

2.2. Calculations of monthly GDD

Based on the daily records from Alishan Weather Station, we calculated the monthly GDD (base temperature 5 °C) for each month between 1969 and 2003 by summing daily degree day values, defined as max ((T_max + T_min)/2 - 5, 0), where max is the maximum function. Over that period, July had the highest average monthly GDD, whereas the mean monthly GDD of January was only about 15% of July’s value (Fig. 2a).

2.3. Height growth data

Between April and July of 2004, 28 trees from a 3-ha Taiwan spruce plantation (established in 1967) located in the study site were selected by stratified sampling based on diameter at breast height and felled at the base (30 cm above the ground). As the study area is now a part of Taiwan’s national park system, the number of trees available to this study was constrained by regulations. The total tree heights of the 28 trees ranged from 4.75 m to 17.5 m. Based on the total height, felled trees were classified as suppressed (height ≤ 10.4 m, eight trees),
codominant (10.4 m < height < 14.2 m, 13 trees), or dominant (height ≥ 14.2 m, seven trees). The average total heights for the three classes were 8.3 m, 12.1 m, and 15.8 m, respectively.

A complete stem analysis was performed on each tree following the procedures outlined in Kariuki (2002). In summary, we first sectioned each tree into 30-cm thick discs. If there was difference in ring numbers between the crown and the base ends of a disc, we split the disc longitudinally through the pith to recover the hidden growth tips (nodal diaphragms). For most of the trees in the dominant and the codominant classes, we were able to recover approximately 80–85% of the hidden growth tips. For trees in the suppressed class, due to growth suppression, we recovered approximately 75% of the hidden tips. We determined the exact year that each recovered growth tip was formed using the protocol given in Kariuki (2002). Among all the recovered hidden tips, the year that each recovered growth tip was formed using the protocol approximately 75% of the hidden tips. We determined the exact year that each recovered growth tip was formed using the protocol given in Kariuki (2002). Among all the recovered hidden tips, the oldest one was formed in 1970, and the youngest one was formed in 2003. For trees in the dominant or the codominant class, the missing tips were all from the first 3–5 and the last 1–2 years. For suppressed trees, the missing tips were all from the first 5–8 and the last 3–4 years. The number of consecutive annual height growth intervals ranged from 19 to 31 (median 30), and 29 to 33 (median 32), for the suppressed, codominant, and the dominant classes, respectively. For each tree, we calculated the annual height growth between the oldest and the youngest recovered growth tips. Annual height growth was defined as the length between two consecutive growth tips, measured to the nearest 1 mm. Cumulative tree height growth curves were then derived from the measured annual height growth (Fig. 3).

2.4. Statistical analysis

The approach used in this study was a combination of growth analysis and nonlinear mixed-effects (NLME) regression. Based on the derived cumulative height growth trends (Fig. 2), we chose a three parameter logistic curve of the form

\[
H(t) = \frac{\text{Asym} \ p \ i}{1 + b \exp(-rt)}
\]

as the height growth trend. In the model, \(H(t)\) is the cumulative tree height (cm) at age \(t\) (years), \text{Asym} \(p\) is the asymptote of the curve (i.e., the ultimate tree height when age approaches infinity), \(b\) is a parameter that relates to the ratio between the ultimate and the initial tree heights (Thornley and Johnson, 2000), and \(r\) is the growth rate parameter (year\(^{-1}\)). Some studies have referred to \(r\) as the initial relative growth rate (e.g., Stoll et al., 1994). For this growth curve, the annual absolute height growth rate is a function of the three parameters and tree age, but is more sensitive to changes in \(r\).

Because the data contained substantial variability among trees and were longitudinal, we used NLME regression to account for the among-tree variations, as well as the within-tree variance and serial correlation structures. Preliminary data analyses suggested that all three parameters of the logistic growth curve should be treated as mixed-effects. In mixed-effects modeling, a fixed effect represents the population average, whereas the associated random effect represents random deviations of individual trees from the fixed effect (Pinheiro and Bates, 2000).

Under NLME modeling, if not affected by any external factors, the cumulative growth curve is given by

\[
H_i(t) = \frac{\text{Asym}_{\text{fixed}} \ p + \text{Asym}_{\text{fixed}} \ i}{1 + (b_{\text{fixed}} + b_i) \exp(-r_{\text{fixed}} + r_i) \cdot t_i} + e_{it},
\]

where \(H_i(t)\) is the height of the \(i\)th tree at age \(t\), \text{Asym}_{\text{fixed}}, b_{\text{fixed}}, \) and \(r_{\text{fixed}}\) are the fixed effects (population averages), \text{Asym}_{\text{fixed}}, b_{\text{fixed}}, \) and \(r_{\text{fixed}}\) are the random effects associated with the \(i\)th tree, and \(e_{it}\) is the random error of the \(i\)th tree at age \(t\).

In our analysis, we assumed that (1) the three random effects jointly have a multivariate normal distribution with a mean of 0 and a variance–covariance matrix of \(\psi; (2) e \sim N(0, \sigma^2 \text{R}), \) where \(\sigma^2\) is the within-tree error variance, and \(\text{R}\) is the within-tree error variance–covariance structure; (3) for different trees, their random effects are independent; and (4) random effects and within-tree errors are independent of each other (Pinheiro and Bates, 2000).

Since height growth of Taiwan spruce is influenced by the temperature conditions during two consecutive years, we used the preceding year’s July to December GDD and the current year’s January to June GDD as the time-varying covariates to explain cumulative growth patterns.

Using a likelihood ratio approach, we first determined the best variance–covariance structure for the three random effects. Then, based on the Akaike information criterion, we determined the effects of dominance class on the three fixed effects. Next, using a backward elimination approach, we selected the GDD variables that affected \(r_{\text{fixed}}\). We assumed that monthly GDD affected \(r_{\text{fixed}}\) only. It is unlikely that GDD variations affected the initial and ultimate heights. Conceptually, we considered that all monthly GDD during the 34-year-period could potentially influence \(r_{\text{fixed}}\). Our goal was to identify which ones indeed had influence and to estimate the magnitudes of those effects. During this phase, whether a monthly GDD should be removed from the model was determined by the marginal contribution of that variable (using Wald F-test, with \(\alpha = 0.05\)). Finally, using a likelihood ratio approach, we accounted for the within-tree variance and autocorrelation structures (\(\text{R}\)) such that the residuals of the final model met the assumption that they are distributed as \(N(0, \sigma^2)\).

We used graphical methods (e.g., residuals diagnostic plots, the observed trends augmented with the fitted trends plots) to assess the adequacy of the final fitted model. All statistical analyses were conducted using R software (R Development Core Team, 2008). For fitting NLME models, we used the \texttt{nlme} function of the \texttt{NLME} package of R (Pinheiro et al., 2008), which estimates the model parameters by maximum likelihood. We used various options available in that package until the residuals of the final model met the equal variance and independence assumptions.
3. Results

3.1. Summary of the final model

In the final model, the best variance–covariance structure ($\psi_i$) for the three random effects was a diagonal matrix (i.e., the three random effects were independent). All three parameters exhibited a considerable degree of tree-to-tree variations (Table 1). The dominance class significantly affected both $\text{Asymp}_{\text{fixed}}$ and $b_{\text{fixed}}$, but not $r_{\text{fixed}}$. Thus, different dominance classes had different population means with respect to $\text{Asymp}_{\text{fixed}}$ and $b_{\text{fixed}}$, but had the same population mean with respect to $r_{\text{fixed}}$. We could view the three dominance classes as trees that already approached their height growth limit (suppressed), are approaching the limit (codominant), and are still in a fast growing phase (dominant).

The within-tree unequal variance was overcome by a combination of an exponential variance function (varExp option in NLME) with tree age as the variance covariate, and a scaling of the within-group variance estimate for each of the dominance classes (varIdent option in NLME). An MA(5) process accounted for the within-tree autocorrelation. Diagnostic plots suggested that the residuals of the final model met all of the assumptions (Fig. 4). The Shapiro-Wilk tests indicated that the three random

<table>
<thead>
<tr>
<th>Table 1</th>
<th>Approximated 95% confidence intervals for the estimated standard deviations of the three random effects, and the fixed effect estimates with standard errors (in parentheses) of the three parameters.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asymp (cm)</td>
</tr>
<tr>
<td>Random effect*</td>
<td>100.23, 140.85, 197.92</td>
</tr>
<tr>
<td>Fixed effect</td>
<td>0.135 (0.004)</td>
</tr>
<tr>
<td>Suppressed</td>
<td>972.84 a (57.78)</td>
</tr>
<tr>
<td>Codominant</td>
<td>1383.46 b (46.42)</td>
</tr>
<tr>
<td>Dominant</td>
<td>1683.29 c (60.73)</td>
</tr>
</tbody>
</table>

* The numbers are the lower bound, the mean, and the upper bound for the estimated standard deviation, respectively.

b Means followed by different letters in the same column differ significantly ($P < 0.01$).

Fig. 4. Residual diagnostic plots for the final model. (a) Standardized residuals vs. fitted values plot with the dashed line being a loess fitted trend, (b) standardized residuals empirical autocorrelation function up to lag 8 with dashed lines representing a set of 95% confidence bounds for no autocorrelation, and (c) residuals normal Q–Q plot with the Q–Q line.
effects and the residuals met the normality assumption (all $P > 0.2$, Fig. 4c). Because the fitted values closely matched the observed values (Fig. 5), we concluded that the model fits satisfactorily. All parameter estimates of the MA(5) process were positive (Table 2). Thus, previous height growths had prolonged influences on subsequent growths. The influences, however, diminished with progressing time.

3.2. Effects of monthly GDD on $r_{\text{fixed}}$

The monthly GDD of the previous July and November, as well as that of the current January and May, had significant influence on $r_{\text{fixed}}$ (Table 3). None of the other monthly GDD had a detectable effect on the height growth of Taiwan spruce. The months with significant influences coincided with the critical stages of terminal bud formation and development. During the modeling processes, the monthly GDD of previous August, September, and December were the first ones to be removed, suggesting that the thermal conditions of those months likely had the least influence on the next year’s height growth.

Of the monthly GDD retained in the final model, that of the preceding July had the greatest influence on $r_{\text{fixed}}$, where a $1^\circ C$-day per day rise ($\approx 10\%$ of the mean level) would increase $r_{\text{fixed}}$ by about 0.6%. Thus, a warmer July would promote the height growth of next year. An increase in the mean GDD level of the current May, the active height growth period, also had a positive effect on the current year’s height growth. A 10% increase in the mean GDD level would increase $r_{\text{fixed}}$ by about 0.4%. In contrast, an increase in the mean GDD level of the previous November or of the current January had a negative effect on height growth. As the two negative effects were small in magnitudes, a 10% increase in the respective mean GDD levels would only result in a 0.1% (November) and 0.05% (January) reduction in $r_{\text{fixed}}$.

4. Discussion

Our results revealed that Taiwan spruce height growth responds to past thermal environment variations in a complex manner. Wilmking et al. (2004) suggested that a warmer climate may have both positive and negative effects for trees at high latitudes. Our study extended the assertion further to include subtropical high altitudes. Temperature can affect height growth directly by acting on terminal bud formation and elongation, and indirectly by changing carbohydrate partitions (Junttila, 1986). Since terminal buds are main carbohydrate sinks, an increase in GDD during the previous and the current growing seasons would enable trees to accumulate a greater amount of carbohydrates and thus promote growth (Kozlowski and Ward, 1957; Pensa et al., 2005). The significant positive effect of a higher mean monthly GDD in July on the next year’s height growth of Taiwan spruce is consistent with studies on conifers at high latitudes or altitudes (e.g., Junttila and Heide, 1981; Junttila, 1986; Gőmöröva and Gőmőry, 1995; Mäkinen, 1998; Mäkinen et al., 2002; Pensa et al., 2005; Gamache and Payette, 2004; Salminen and Jalkanen, 2005; Pensa et al., 2006).

We also found that, like other high latitude conifers (Kanninen, 1985; Perala, 1985; Jones et al., 1991; Salminen and Jalkanen, 2005), a warmer environment during the early part of the growing season facilitates the leader shoot elongation of Taiwan spruce. For many temperate species, the beginning of bud burst and leafing is closely related to the spring thermal regime (e.g., Sparks et al., 1998).

**Table 2**

Approximated 95% confidence intervals for the estimated parameters of the MA(5) process.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>LCL</th>
<th>Estimate</th>
<th>UCL</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\theta_1$</td>
<td>0.92</td>
<td>1.15</td>
<td>1.39</td>
</tr>
<tr>
<td>$\theta_2$</td>
<td>0.78</td>
<td>1.08</td>
<td>1.39</td>
</tr>
<tr>
<td>$\theta_3$</td>
<td>0.57</td>
<td>0.77</td>
<td>0.99</td>
</tr>
<tr>
<td>$\theta_4$</td>
<td>0.26</td>
<td>0.34</td>
<td>0.42</td>
</tr>
<tr>
<td>$\theta_5$</td>
<td>0.08</td>
<td>0.17</td>
<td>0.25</td>
</tr>
</tbody>
</table>

*LCL and UCL denote the lower and the upper confidence limits, respectively.*

**Table 3**

Estimated marginal effects ($\text{year}^{-1} \cdot \text{C-day}^{-1} \times 10^{-5}$) and standard error (in parentheses, $\times 10^{-5}$) for the monthly GDD variables affecting $r_{\text{fixed}}$.

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Estimate</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Previous</td>
<td>July</td>
<td>2.46 (0.70)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>November</td>
<td>−0.96 (0.17)</td>
<td></td>
</tr>
<tr>
<td>Current</td>
<td>January</td>
<td>−1.13 (0.35)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>2.09 (0.45)</td>
<td></td>
</tr>
</tbody>
</table>

*Of the monthly GDD retained in the final model, that of the preceding July had the greatest influence on $r_{\text{fixed}}$, where a $1^\circ C$-day per day rise ($\approx 10\%$ of the mean level) would increase $r_{\text{fixed}}$ by about 0.6%. Thus, a warmer July would promote the height growth of next year. An increase in the mean GDD level of the current May, the active height growth period, also had a positive effect on the current year’s height growth. A 10% increase in the mean GDD level would increase $r_{\text{fixed}}$ by about 0.4%. In contrast, an increase in the mean GDD level of the previous November or of the current January had a negative effect on height growth. As the two negative effects were small in magnitudes, a 10% increase in the respective mean GDD levels would only result in a 0.1% (November) and 0.05% (January) reduction in $r_{\text{fixed}}$.***
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