

EFFECTS OF SPATIAL AUTOCORRELATION ON INDIVIDUAL TREE GROWTH MODEL OF *PICEA LIKIANGENSIS* FOREST IN NORTHWEST OF YUNNAN, CHINA

X. Cheng¹, Y. Wang¹, W. Li², H. Gong¹, S. Wang¹ and S. Wang^{3,*}

¹. Department of Geography and Ecology, Southwest Forestry University, Kunming 650224, Yunnan, China

². Yunnan Academy of Biodiversity, Southwest Forestry University, Kunming 650224, Yunnan, China

³. College of Landscape Architecture, Southwest Forestry University, Kunming 650224, Yunnan, China

*Corresponding Author E-mail: xipingcheng@yahoo.co.jp

ABSTRACT

We established a permanent plot located at *Picea likiangensis* forest in Shangri-La county, northwest of Yunnan province, China, from 2008 to 2012, and recorded all stems with the diameter at breast height (DBH) ≥ 5 cm, mapped the positions of corresponding stem bases. Because *Picea likiangensis* (Franch.) Pritz. Was a dominant species, it was specifically measured. We used Bayesian statistical approach to quantify a spatially autocorrelated random effects. Meanwhile, the effect of competition on individual growth was also considered. The results showed that symmetrical competition played a very important role in affecting individual growth. When spatially autocorrelated random effects were included, the model accounted for a significant proportion of the variation ($R^2 = 0.87$; $P < 0.001$). We also analyzed collected data of other tree species found in the plot, and a high level of correlation relationship was consistently found when spatial autocorrelation was included. The Bayesian approach used in this study, including the intrinsic CAR model, is a powerful technique for exploring important ecological information from forest census data. Our model for the measurement of tree growth rate may be used to simulate forest dynamics and to improve the management practices of natural forests.

Keywords: Bayesian statistics, growth model, inter-individual competition, *Picea likiangensis* forest, spatial autocorrelation.

INTRODUCTION

Estimation of demographic data on tree growth is important for predicting population dynamics and growth conditions of the whole forest, and for understanding the ecological characteristics of trees. Meanwhile, it is also important for appropriate forest management (Kobe and Coates, 1997; Umeki, 2001; Cheng *et al.*, 2012). However, researchers tend to use tree height, diameter at breast height, soil organic matter, light environment and many other measurable factors to construct tree growth models (de Reffye *et al.*, 1995; Martin-Benito *et al.*, 2008; Cheng *et al.*, 2011). Although unknown and immeasurable factors might cause differences in the growth of trees even when they are from the same habitat, and an aggregation distribution of forest trees could form so called spatial autocorrelation phenomenon (Legendre and Legendre, 1998), random effect is often neglected when trees growth model is constructed, which results in too large or to small predictive values when random effects related to forest spatial autocorrelation are neglected (Fukasawa *et al.*, 2009). Although some studies have started to consider the effect of spatial autocorrelation (Fox *et al.*, 2001; Shi and Zhang, 2003), using this method to explore the spatial

random effect on tree growth has not become popular in tree growth model with the spatial autocorrelation effect considered. Actually, the effect of spatial autocorrelation on tree growth model may not only predict essential factors that affect forest tree growth using data related to individual distribution of trees, but also provide new ideas for forest research.

Competition between individuals cannot be ignored in the tree's growth process, we paid special attention to the degree of asymmetry of competition among individual trees, which can be used to explore the type of resources trees are competing for. Competition often tends to be symmetric when the resource is under the ground (e.g., water or nutrients), and it tends to be asymmetric when the resource is above ground (e.g., light; Weiner, 1990; Schwinning and Weiner, 1998). Thus, the major resources trees are competing for can be explored by assessing the degree of asymmetry in competition.

In this study, we analyzed the initial data on the growth of trees, competition among individuals, and the spatial autocorrelation in tree growth model. We also used Gaussian intrinsic conditional autoregressive model (intrinsic CAR) to discuss the necessity and feasibility of spatial autocorrelation in tree growth model.

MATERIALS AND METHODS

Study area: We collected data on tree growth from a permanent plot in the *Picea likiangensis* forest in Shangri-La county in northwestern Yunnan province, China (27°50' N, 99°42' E; Figure. 1). This area is in the cold temperate zone characterized by a monsoon climate. The vegetation type is cold temperate coniferous forest, which is also called dark coniferous forest. The altitude ranges from 3350 to 3696 m above sea level. Due to the high altitudes, winters are chilly but sunny. The mean annual temperature is 5.4 °C. It is 13.3 °C in the hottest month (July) and -3.8 °C in the coldest month (December). The mean annual precipitation is 607 mm, of which 70% occurring in June-September. Evaporation is 1671 mm and relative humidity is 70%. The soil type is mainly dark brown forest soil.

Our target species was *Picea likiangensis* (Franch.) Pritz., a common conifer species found in this region. In the survey plot, this type species always located in low-lying areas and places with good water conditions. Species present in the understory of *Picea likiangensis* forests include *Sorbus rufopilosa* C. K. Schneid., *Abies georgei* Orr., *Larix potaninii* var. *macrocarpa*, *Quercus aquifoloides* Rehd. et Wils., *Quercus spinosa* David ex Fr., *Betula platyphylla* Suk., *Abies forrestii* C. C. Rogers, *Quercus pannosa* Hand.-Mazz., *Betula albo-sinensis* Burk., *Acer forrestii* Diels., and *Sorbus vilmorinii* C. K. Schneid., *Bothrocaryum controversum*, *Rhododendron simsii* Planch.

Data collection: We established a permanent rectangular plot (100m × 100m) in 2008. We mapped the positions of the bases of all stems ≥ 5 cm in diameter at breast height (DBH) in the plot using a surveying compass (S-27; Ushikata, Yokohama, Japan) and an ultrasonic range finder (Vertex III; Haglof, Sweden). We identified them at the species level. We measured the DBH of all stems in 2008 and 2012 (Table 1). Considering some target trees were found at the edge of the fixed standard area and thus the neighbor trees may be present outside, we did edge corrections when the data are processed (Cheng et al., 2012; 2014). In this study, we regarded the area within 10 m from each edge as the buffering area. Therefore, the corrected standard area was 80 m × 80 m. To analyze spatial autocorrelation and competition coefficient, we regarded all trees inside the corrected standard area as targets and those in the buffering areas as neighbors. We chose the *Picea likiangensis* as the targets, because this species was the most abundant. We also inspected the other four tree species and analyzed the spatial autocorrelation and the construction of individual competition model while considering the influence of all the surrounding trees.

Data analysis: Individual competition

The basal area (BA) of tree was used in this study to represent the competition among individuals and to distinguish symmetrical competition from asymmetrical competition. The asymmetrical competition was used to calculate the basal area of all other individuals within the radius of 10 m whose BA was greater than that of the target individual; whereas the symmetrical competition was used to calculate the basal area of the individuals of all BAs within this range. The equation of individual competition was based on Collet and Chenost (2006):

$$C = \int_0^{D_{max}} \frac{\pi}{4} x^2 f(x) dx \quad (1)$$

Where C is the individual competition index; x is DBH; D_{max} and $f(x)$ are the maximum DBH and the frequency of x respectively.

For the calculation of individual competition, the individual which is considered the edge effect of buffer should be incorporated into the calculation of neighborhood individual, rather than being incorporated into the calculation of target individual.

Modeling spatial autocorrelation

Forest spatial autocorrelation refers to the growth of trees in the space of pros and cons, because individuals tend to live together (Fukasawa et al., 2009). The clumped distribution may be due to species dispersing ability between habitats, species competition dispute, chemical disturbance or species formation (Miller et al., 2007). Because of the uncertainty, it will exhibit similar inclination closer and different growth trend in the space (Cheng et al., 2014).

To specify the spatially autocorrelated random effect, we employed a Gaussian intrinsic conditional autoregressive model (intrinsic CAR; Besag et al., 1991; Ishihama et al., 2010) in a framework of hierarchical Bayesian statistics. The CAR model is one of the methods giving the best performances in exploring spatial autocorrelation (Dormann et al., 2007; Beale et al., 2010). We divided the plots into 10 m × 10 m blocks and assumed that the conditional distribution of the spatial random effect S_i for block i depends on the spatial random effect of the neighboring blocks of i . In this study, the intrinsic CAR model for the spatial random effect at block i was given by a conditional distribution:

$$S_i | S_j \sim N\left(\frac{\sum_{j \in \delta i} a_{ij} S_j}{n}, \frac{\sigma^2}{n}\right) \quad (2)$$

$$N\left(\frac{\sum_{j \in \delta i} a_{ij} S_j}{n}, \frac{\sigma^2}{n}\right)$$

Where N denotes the Gaussian distribution

$$\frac{\sum_{j \in \delta_i} a_{ij} S_j}{\sigma^2}$$

with a mean n and an inverse variance n . δ_i is the set of neighboring blocks associated with block i , and block i per se is not included in the set. $j \in \delta_i$ means it's can be calculated only when the block i is adjacent to block j . When the target block adjacent to i and j shares the same boundaries, the parameter $a_{ij} = 1$; otherwise, $a_{ij} = 0$. Neighboring blocks that share an edge or a diagonal corner with block i are included in δ_i . S_i follows a normal distribution in which the expectation value is the average of the values of neighboring blocks. Note that this assumes that the autocorrelation between neighboring blocks is positive. n is the number of blocks neighboring block. We assigned non-informative priors as $\sigma^2 \sim \text{gamma}(0.0001, 0.0001)$. The spatially autocorrelated random effect was assumed to be the same across species.

The spatially explicit model described above can be fitted to the data using software WinBUGS (Spiegelhalter et al., 2004). To capture only important patterns in the data, we selected the best model from some candidate models using the DIC.

Modeling basal area growth rate

The basal area (BA) for each individual was calculated from the DBH assuming that the stem cross-section was a circle. The growth model we used in this study is an extension of the general functional form of individual plant growth proposed by Yokozawa and Hara (1992). The general function form was altered to express basal area growth and to assess the effect of competition by neighbors:

$$G(t, w) = a_0 w + a_1 w^m + c_1 w C(t, w) + c_2 w C(t, w_0) \quad (3)$$

Where $G(t, w)$ is the average of the absolute growth rate at time t , whose basal area is w . $C(t, w)$ is the cumulative value of basal area of all individuals whose basal area is greater than w ; w_0 is the minimum standard of individual basal area; a_0, a_1, c_1, c_2, m are parameters.

$C(t, w)$ is the inhibition of expression of individual growth that the ones whose the basal area are greater than w effect on the ones which are w , that is asymmetric competition, however $C(t, w_0)$ is symmetric competition which is not distinguishing individual size. We modified equation (3) to obtain the following model:

$$G(B) = a_1 B + a_2 B \ln(B) + a_3 C(B) + a_4 C(B_0) + S \quad (4)$$

Where B is the basal area and $G(B)$ is the basal area annual growth, B_0 is the minimum standard of individual basal area, $C(B)$ is the asymmetric competition and $C(B_0)$ is the symmetric competition, a_1, a_2, a_3, a_4 are parameters.

It can be seen in equation (4) that the original form of the general growth function (Eq. 3) has been modified, in which we converted the second term to $B \ln(B)$, adjusted the third term to asymmetric competition $C(B)$, and adjusted the fourth term to symmetric

competition $C(B_0)$. In equation (3), we introduced the random effects of the spatial structure, which is spatial autocorrelation coefficient S . Parameters a_1, a_2, a_3, a_4 can be derived from the model adjustment calculus. Because the performance of intrinsic CAR model could be improved by the process of model selection (Beale et al., 2010), we conducted a model selection by backward elimination with the deviance information criterion (DIC) (Spiegelhalter et al., 2002). We started from the full model (Eq.4) and omitted irrelevant predictor variables until a model with the lowest DIC was obtained. We targeted five kinds of dominant species and constructed for each species growth model in considering and ignoring spatial autocorrelation.

RESULTS AND DISCUSSION

Relationship between growth and competition: Through the analysis of individual growth and competition, symmetric competition and asymmetric competition were based on the posterior means (Table 2), the growth of *Picea likiangensis* individual for the surrounding individual asymmetric competition a_3 showed a positive value (0.00576) according to the characteristics of asymmetric competition of individuals, indicated that the growth of *Picea likiangensis* weak in the light environment due to individual competition reasons, but it contains zero at the 95% confidence intervals (-0.00114, 0.00638), indicating that this feature was not statistically significant. On the other hand, the symmetric competition a_4 was a negative value (-0.00594), and there was no zero in the 95% confidence intervals (-0.00783, -0.000986). Therefore, these results generally agreed with the expectation that intense competition for the underground resources (water, organic nutrients), which are consistent with findings by the other researchers (Liu et al., 2003, Cheng et al., 2014).

Spatial autocorrelation: The results of spatial autocorrelation analysis were shown in Figure 2. The individuals of annual growth larger for basal area mainly concentrated in the blocks, with spatially autocorrelation random effect as positive (0 ~ 6.4). Spatial distribution map of spatial autocorrelation can accurately determine the distribution of individual growth conditions in the space. The determination coefficient for considering spatial autocorrelation model ($R^2 = 0.87^{***}$) was greater than that when ignoring spatial autocorrelation model ($R^2 = 0.72^{***}$). Using spatial autocorrelation growth model to predict basal area annual growth condition was more relevant for handling the measured data (Figure 3), with similar results obtained for the analysis of other tree species found in the study area (Table 3). When considering factors that affect individual growth process, factors such as topography,

geology, soil and light environment could be determined (fixed effects), and factors that could not be determined (random effects), such as spatial autocorrelation random effect, would generally be ignored. However, our

simulation results clearly show that when factors related to spatial autocorrelation efficacy are considered, the accuracy of the construction of tree growth model could be greatly improved.

Table 1. Mean values of tree height, mean diameter at breast height (DBH), and mean basal area (BA) growth rate for major species in study area.

Species	N	Mean height (m) in 2008	Mean DBH (cm) in 2008	Mean DBH (cm) in 2012	Mean BA growth ($\text{cm}^2 \text{yr}^{-1}$)
<i>Picea likiangensis</i>	267	21.7	26.7	31.6	8.3
<i>Sorbus rufopilosa</i>	74	7.1	8.1	9.4	1.2
<i>Abies georgei</i>	51	12.8	14.7	17.7	5.8
<i>Quercus aquifolioides</i>	42	15.6	16.5	22.3	10.7
<i>Larix potaninii</i>	28	27.6	23.4	27.8	7.8
Others species	62	6.7	7.6	9.2	3.1

Table 2. Estimates the final model of *Picea likiangensis* for the parameters

Parameter	Posterior means	SD	95% credible intervals
a_1	0.257	0.0326	(0.164, 0.276)
a_2	-0.0362	0.00952	(-0.0518, -0.000927)
a_3	0.00576	0.000859	(-0.00114, 0.00638)
a_4	-0.00594	0.000887	(-0.00783, -0.000986)

*: a_1 , a_2 , a_3 and a_4 are parameters in the selected model: $G(B) = a_1B + a_2B \ln(B) + a_3C(B) + a_4C(B_0) + S$

Table 3. Correlation values of models consider and ignore spatial autocorrelation for main tree species

Species	R^2	
	Consider the spatial autocorrelation random effect	Ignore the spatial autocorrelation random effect
<i>Picea likiangensis</i>	0.87***	0.72***
<i>Sorbus rufopilosa</i>	0.81**	0.72*
<i>Abies georgei</i>	0.73*	0.60*
<i>Quercus aquifolioides</i>	0.92***	0.84***
<i>Larix potaninii</i>	0.64**	0.58**

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$

Evaluation of growth model: The selected model was based on the deviation information criterion (DIC). For the full model (Eq.4), DIC=1875.2, and DIC values of the candidate models were greater than the full model (eg. ignore asymmetric competition $C(B)$ DIC=1895.4, ignore the symmetric competitive $C(B_0)$ DIC=1887.6). Therefore, the full model was determined as the final model. The parameters a_1 , a_2 in the final model that posterior means were positive (0.257) and negative (-0.0362), respectively (Table 2), and the 95% confidence intervals did not contain zero. The results show that during the basal area growth process of *Picea likiangensis* individuals, the individual initial value was greater and the growth rate was faster (basal area $< 180\text{cm}^2$). When the individuals grew to some extent (basal area $> 180\text{cm}^2$), the growth rate displayed a decreasing trend (Figure 4). According to the predicted

final model by using WinBUGS software, posterior means and the mean of spatial autocorrelation random effect, the variance of the value was small in the average coverage of 80%, which showed that the predicted data were relatively credible by spatial autocorrelation. R-hat was calculated in various Markov Chain Monte Carlo (MCMC) software including WinBUGS (Gelman and Kenneth, 2011), and the results also indicated that the convergence and stability of the final model was achieved (i.e., the parameters of R-hat values are closed to 1, and less than 1.1) (Gelman et al., 2004). In general, previous tree growth models without considering the spatial autocorrelation random effect which were based on environmental factors such as the underground and the ground resource data, and might accurately predict the tree growth to some extent (Cheng et al., 2011). However, here more factors are considered, including

tree growth, space position, and the spatial autocorrelation random effects, are they could help more

accurately predict the individual growth of trees.



Figure 1. Location of study area.

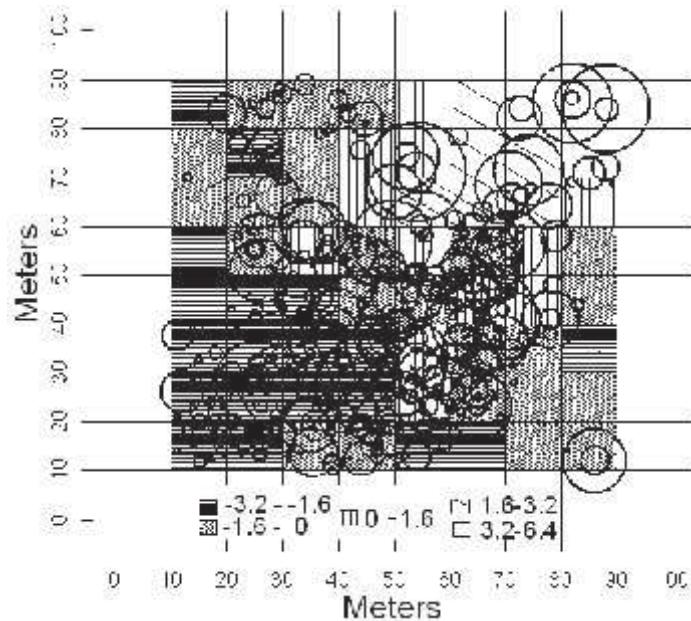


Figure 2. Spatial map of the posterior means for spatial autocorrelation random effect. Density of patterns represent the change in BA growth rate by the spatially autocorrelated random effect. Symbols represent positions of trees. The size of the symbols correlates with the measured growth rate (i.e., the larger the symbol, the larger the growth rate).

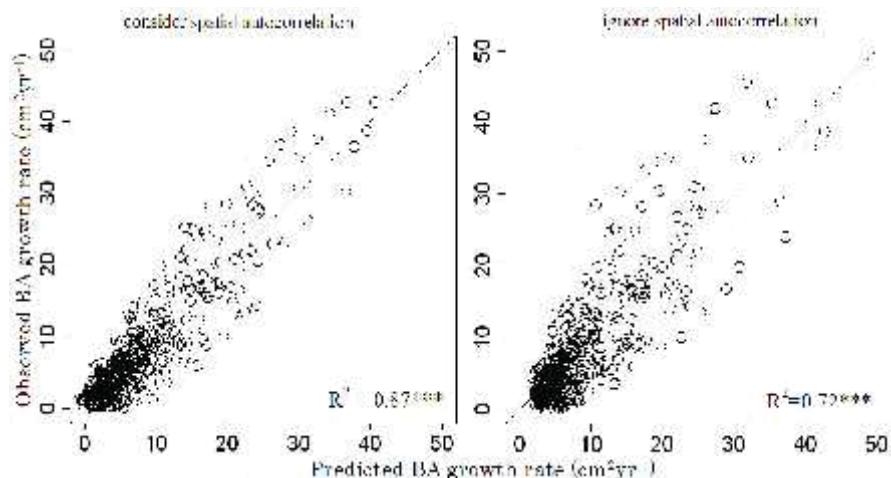


Figure 3. Relationship between observed BA growth rate and BA growth rate predicted by the final model. The solid line represents the 1:1 relationship.

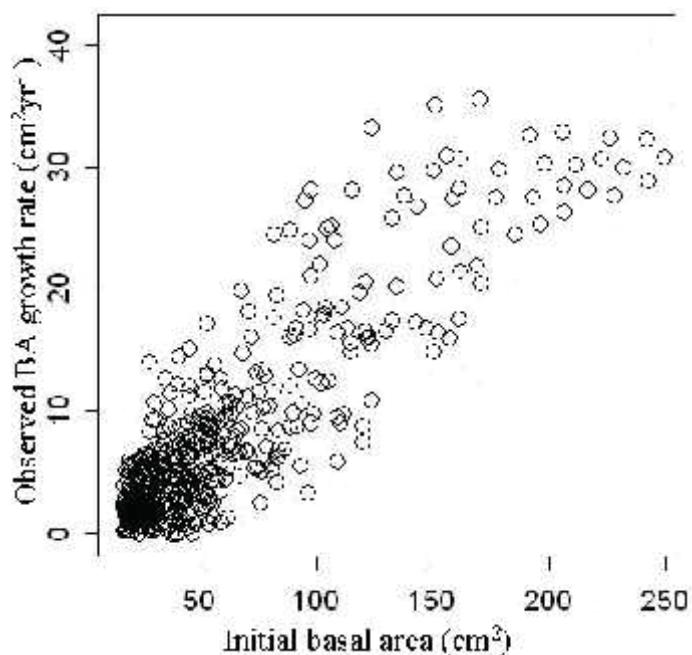


Figure 4. Relationship between initial basal area and observed growth rate.

Conclusion: The forest trees during the growth process will be affected by some unmeasured factors, and similar tendency also happens in the closer space. In this paper, models that included the spatially autocorrelated random effect (S) had much lower DIC's than models that did not include S (Table 3). This indicates that when spatially autocorrelated random effects were included, the model accounted for a significant proportion of the variation. The Bayesian hierarchical analysis presented here has quantified parameters of multi species. It suggests that the existence of unknown environmental factors might have influenced the growth rate of trees according to intrinsic CAR model. The purpose of this study is to use Bayesian statistical method and the spatial

autocorrelation model to improve the precision of fitting tree growth model (Figure 3), and the results show that by considering the spatial autocorrelation random effect, the accuracy of the constructed model could be improved (Table 3), and the Spatial autocorrelation has been considered in several aspects of ecological studies. A lot of researches recently analyzed the spatial structure of forests, but they mainly focused on the stand structure and distribution patterns (Tang, 2010; Cheng et al., 2012). In contrast, very few studies use tree spatial distribution, especially spatial autocorrelation to construct statistical model (Lippitt et al., 2008), and those models are dominantly based on measurable environmental conditions. In this study unknown environmental factors

were used in the spatial autocorrelation model to predict the growth of individual trees, which could help shorten the circle of fieldwork and reduce the cost. It is shown that the spatial autocorrelation model is not only an efficient tool for analyzing spatial distribution, but also an effective way for predicting tree growth tendency. Spatial autocorrelation random effects can be used to analyze a specific species or multiple species when the hierarchical Bayesian model is applied, and to investigate the ecological niches of multiple species.

Acknowledgments: This study was supported by National Natural Science Foundation of China (31360164), and Scientific Research Foundation of Southwest Forestry University (111301).

REFERENCES

- Beale, C.M., J.J. Lennon, J.M. Yearsley, M.J. Brewer, D.A. Elston (2010). Regression analysis of spatial data. *Ecol. Lett.* 13:246–264.
- Besag, J., J. York, A. Mollier (1991). Bayesian image restoration with two applications in spatial statistics (with discussion). *Ann. I. Stat. Math.* 43:1–59.
- Cheng, X., K. Umeki, T. Honjo, P. Shao (2011). Height growth, diameter-height relationships and branching architecture of *Pinus massoniana* and *Cunninghamia lanceolata* in early regeneration stages in Anhui Province, eastern China: effects of light intensity and regeneration mode. *Forest Science and Practice* 13(1):1-12.
- Cheng, X., Y. Wang, X. Yang, H. Gong (2012). Stand Structure of Natural *Pinus-Cunninghamia* Forest in Anhui, Eastern China. *Bulg. J. Agric. Sci.* 18(6): 997-1004.
- Cheng, X., K. Umeki, T. Honjo, D. Mizusaki (2014). Basal area growth rates of five major species in a *Pinus-Cunninghamia* forest in eastern China as affected by asymmetric competition and spatial autocorrelation. *J. For. Res.* 19(1): 86-96.
- Collet, C. and C. Chenost (2006). Using competition and light estimates to predict diameter and height growth of naturally regenerated beech seedlings growing under changing canopy conditions. *Forestry* 79(5): 489-582.
- deReffye, P., F. Houllier, F. Blaise, D. Barthélémy, J. Dauzat, D. Auclair (1995). A model simulating above- and below-ground tree architecture with agroforestry applications. *Agroforest Syst.* 47 (1): 175-197.
- Dormann, C.F., J.M. McPherson, M.B. Araujo, R. Bivand, J. Bolliger, G. Carl, R.G. Davies, A. Hirzel, W. Jetz, W.D. Kissling, I. Kuhn, R. Ohlemüller, P.R. Peres-Neto, B. Reineking, B. Schroder, F.M. Schurr, R. Wilson (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628.
- Fox, J.C., P.K. Ades, H. Bi (2001). Stochastic structure and individual tree growth models. *Forest Ecol. Manag.* 154(1): 261-276.
- Fukasawa, K., F. Ishihama, H. Oguma, T. Takeda, N. Tanaka, A. Takenaka (2009). Analyses for distributions of organisms considering spatial autocorrelation using the conditional autoregressive models (in Japanese with English abstract). *The Ecological Society of Japan* 59 (2): 171-186.
- Gelman, A., J.B. Carlin, H.S. Stern, D.B. Rubin (2004). Bayesian data analysis, 2nd eds. Champan and Hall; Boca Raton. pp. 246-268.
- Gelman, A. and S. Kenneth (2011). Handbook of Markov Chain Monte Carlo. 1stEd. Chapman & Hall/CRC; London. pp. 163-174.
- Ishihama, F., T. Takeda, H. Oguma, A. Takenaka (2010). Comparison of effects of spatial autocorrelation on distribution predictions of four rare plant species in the Watarase wetland. *Ecol. Res.* 25:1057–1069.
- Kobe, R.K. and K.D. Coates (1997). Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. For. Res.* 27 (2):227-236.
- Legendre, P. and L. Legendre (1998). Numerical Ecology. Elsevier: Amsterdam. pp. 147-159.
- Lippitt, C.D., J. Rogan, J. Toledano, F. Sangermano, J.R. Eastman, V. Mastro, A. Sawyer (2008). Incorporating anthropogenic variables into a species distribution model to map gypsy moth risk. *Ecol. Modell.* 210(3):339-350.
- Liu, Q., Y. Wu, N. Wu (2003). Forest gap characteristic in a coniferous *Picea likiangensis* forest in the Yulong Snow Mountain Natural Reserve, Yunnan Province, China (in Chinese with English abstract). *Chinese J. Appl. Ecology* 14(6): 845-848.
- Martín-Benito, D., G. Gea-Izquierdo, M. del Río, Isabel Cañellas (2008). Long-term trends in dominant-height growth of black pine using dynamic models. *Forest Ecol. Manag.* 256(5): 1230-1238.
- Miller, J., J. Franklin and R. Aspinall (2007). Incorporating spatial dependence in predictive vegetation models. *Ecol. Modell.* 202 (3): 225-242.
- Schwinning, S. and J. Weiner (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113(4): 447-455.

- Shi, H. and L. Zhang (2003). Local analysis of tree competition and growth. *Forest Sci.* 49(6): 938-955.
- Spiegelhalter, D.J., N.G. Best, B.R. Carlin, A. van der Linde (2002). Bayesian measures of model complexity and fit. *J. Roy. Stat. Soc. B. Met.* 64 (4): 583-639.
- Spiegelhalter, D.J., A. Thomas, N.G. Best, D. Lunn (2004). WinBUGS version 1.4 user manual. MRC Biostatistics Unit: Cambridge. pp. 186-194.
- Tang, M. (2010). Advances in study of forest spatial structure (in Chinese with English abstract). *Scientia Silvae Sinicae* 46(3): 117-122.
- Umeki, K. (2001). Growth characteristics of six tree species on Hokkaido Island, northern Japan. *Ecol. Res.* 16 (3):435-450.
- Weiner, J. (1990). Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5 (11): 360-364.
- Yokozawa, M. and T. Hara (1992). A canopy photosynthesis model for the dynamics of size structure and self-thinning in plant populations. *Ann. Bot.* 70 (4): 305-316.

Copyright of JAPS: Journal of Animal & Plant Sciences is the property of Knowledge Bylanes and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.