



# Effectively tuning plant growth models with different spatial complexity: A statistical perspective



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## ABSTRACT

Forest gap models (non-spatial, patch- and individual-based models) and size structure models (non-spatial stand models) rely on two assumptions: the mean field assumption (A-I) and the assumption that plants in one patch do not compete with plants in other patches (A-II). These assumptions lead to differences in plant size dynamics between these models and spatially explicit models (or observations of real forests). Therefore, to more accurately replicate dynamics, these models require model tuning by (1) adjusting model parameter values or (2) introducing a correction term into models. However, these model tuning methods have not been systematically and statistically investigated in models using different patch sizes.

We used a simple spatially explicit model that simulated growth and competition processes, and rewrote it as patch models. The patch sizes of the patch models were set between 4 and 1500 m<sup>2</sup>. First, we estimated the parameter values (the intrinsic growth rate, metabolic loss, competition coefficient, and competitive asymmetry) of these models that best reproduce plant size growth under competition using field data from a Sakhalin fir stand, and compared the parameter values among the models. Second, we introduced correction terms into the patch models and estimated the optimal correction term for reproducing plant size growth under competition using the field data.

The estimated parameter values of the patch models for all patch sizes differed greatly from those of the spatially explicit models. Therefore, parameter values should not be shared between spatially explicit models and patch models. In addition, the parameter value sets for the models with small patches differed from those with large patches. This is because parameter values for small patches mainly improve biases of A-II, while those for large patches mainly improve biases of A-I. Therefore, parameter values should not be shared between patch models with small patches and with large patches.

The estimated correction term in the patch models with large patches excluded the competitive effects of small and medium-sized plants on their neighbors, even though these effects exist in real stands. This exclusion can be ascribed to the discrepancy between their competition in real plant populations and A-I. Therefore, the competitive effects of small and medium-sized plants should not be included in patch models with large patches. Finally, the reproducibility of the models tuned with correction terms was higher than those with adjusted parameters.

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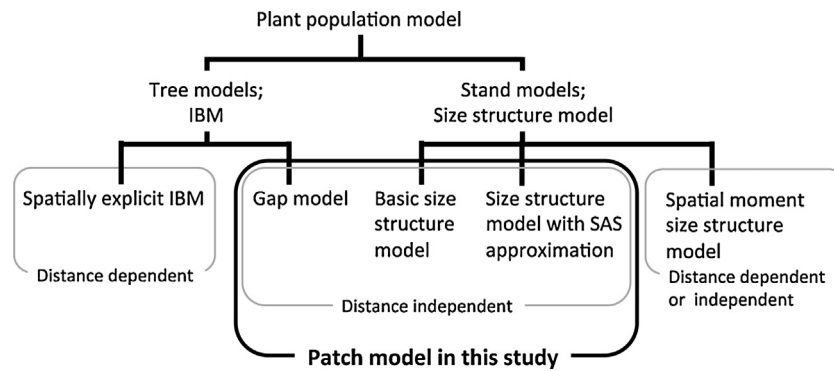
## 1. Introduction

Simulation models of plant populations are effective tools that can integrate plant population processes and predict the results of their interactions. In this study, we focused on gap and size structure models. Gap models (e.g., Botkin et al., 1972; Shugart and

West, 1977; Prentice and Leemans, 1990) are non-spatial (i.e., distance independent) patch-based individual-based models (IBMs) (see Fig. 1) and are well established and often used for predicting the dynamics of forests. There are some types of size structure models (see Fig. 1). Basic size structure models (e.g., Nagano, 1978; Takada and Iwasa, 1986; MINoSGI: Toda et al., 2009) are non-spatial stand models that simulate the temporal change in plant size distribution. Size-structure models with size- and age-structured (SAS) approximation (Kohyama, 1993; Moorcroft et al., 2001; Kohyama, 2005) are size structure models with multiple small patches like gap

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**Fig. 1.** Classification of the models discussed in this study.

The models discussed in this study were classified following [Porté and Bartelink \(2002\)](#). They classified plant population models into two groups: 'tree models,' in which single trees represent the most detailed level of modeling, and 'stand models,' in which the stand constitutes the smallest unit of modeling. Individual-based models (IBMs) are classified as tree models while size structure models are classified as stand models. IBMs simulate recruitment, growth, death, and competition processes for each individual, while size structure models simulate the temporal change in plant size distribution. The authors further divided the stand and tree models into 'distance-dependent' and 'distance-independent' models. Spatially explicit models (e.g., SORTIE: [Pacala and Deutschman, 1995](#); SEIB-DGVM: [Sato et al., 2007](#)) are classified as distance-dependent IBMs. These models can simulate the local interactions among individual trees within a spatially explicit virtual forest. Gap models (e.g., [Botkin et al., 1972](#); [Shugart and West, 1977](#); [Prentice and Leemans, 1990](#)) are classified as distance-independent (or non-spatial and patch-based) IBMs. The basic size structure model (e.g., [Nagano, 1978](#); [Takada and Iwasa, 1986](#); MINOSGI: [Toda et al., 2009](#)) and the size structure model with size- and age-structured (SAS) approximation (e.g., [Kohyama, 1993](#); [Moorcroft et al., 2001](#); [Kohyama, 2005](#)) are classified as distance-independent size structure models. Size structure models with SAS approximation introduce patches and their age structure into the basic size structure model. In this model, there is an age for each patch, which is reset by disturbance. This model simulates not only the temporal change in size distribution but also that of age distribution of patches, and does not calculate the magnitude of the competitive effect (or the amount of resources) for each patch, but calculates that of patches of the same age. Spatial moment size structure models (e.g., [Kubo et al., 1998](#); [Adams et al., 2013](#)) are the size structure model incorporating the spatial moment approximation ([Bolker and Pacala, 1997](#); [Law and Dieckmann, 2000](#); [Murrell et al., 2004](#)) and are classified as distance-dependent or distance-independent size structure models. These models introduce the second moment into basic size structure models. In these models, the first moment is the density of plants for each plant size, which can be simulated by a basic size structure model, and the second moment is the density of pairs of competing plants of different sizes. Frequently, the vector connecting the locations of the two plants (i.e., the direction and distance from one individual to another) is introduced into the second moment, which, in this case, is defined as the density of pairs of individuals of different sizes for each vector. In this study, we refer to the gap model, the basic size structure model, and the size structure model with SAS approximation generically as 'patch models.'

models. Recently, simulation models of plant populations have been applied at a global scale to create the dynamic global vegetation model (DGVM), but IBMs usually incur enormous computational costs. Reducing these computational costs is necessary ([Purves and Pacala, 2008](#); [Strigul et al., 2008](#); [Haverd et al., 2014](#)). Size-structure models are considered among the most powerful methods for reducing computational costs ([Moorcroft et al., 2001](#); [Purves and Pacala, 2008](#)). Additionally, basic size structure models have only one relatively large patch while gap models and size structure models with SAS approximation have multiple relatively small patches (100–1000 m<sup>2</sup>; [Liu and Ashton, 1995](#)). Therefore, the latter models can simulate spatial inhomogeneity within plots. The basic size structure model and the size structure model with SAS approximation are distance-independent (non-spatial) models ([Porté and Bartelink, 2002](#)). In this study, we refer to these models generically as 'patch models' (see [Fig. 1](#)).

Patch models rely on two unrealistic assumptions ([Bugmann, 2001](#)). The first assumption is that individual plants encounter one another in proportion to their mean abundance across space ([Law et al., 2000](#)), which is referred to as the mean-field assumption (A-I). The second assumption is that plants in one patch (also known as a plot or gap) do not compete with plants in other patches (A-II). The assumption A-I does not hold true for most plant populations because plants are sessile and compete only with their neighbors ([Law et al., 2000](#); [Lischke et al., 2007](#)). Moreover, the assumption A-II does not hold true in most plant populations where there is no buffer area between patches. Therefore, these assumptions can decrease the reproducibility of models for plant size dynamics ([Pacala and Deutschman, 1995](#)). If these assumptions remain in models, it is necessary to conduct model tuning to more accurately reproduce plant size dynamics. There are two main methods of model tuning: (1) parameter adjustment and (2) introducing a correction term into the model. Correction terms correct for the strength of competition between plants of different sizes, which play the similar role as the second moment (i.e., the density of pairs

of plants of different sizes for each vector connecting the locations of the two plants) in the spatial moment size structure model ([Kubo et al., 1998](#); [Adams et al., 2013](#); see also [Fig. 1](#)). Some traditional patch models often use approximately true values obtained from field measurements as parameter values (e.g., FORSKA: [Prentice and Leemans, 1990](#); HYBRID v3.0: [Friend et al., 1997](#)). These model tunings have not been systematically and statistically investigated in patch models with various patch sizes.

In this study, we examined the issues concerning the tuning of growth sub-model in patch models to reproduce plant size growth under competition. First, we examined optimal parameter values and correction terms for each patch size. Then, we examined whether the optimal parameter values of the spatially explicit model should be used as parameters in patch models in terms of reproducibility; that is, we discussed whether parameter values derived from the plant population that does not rely on assumptions A-I and A-II should be applied to patch models. Next, we examined the possibility of applying the same parameter values or correction terms from one patch size to other patch sizes. Finally, we compared parameter adjustments with the introduction of a correction term to determine the best model tuning method.

To address these concerns, we used the individual-based mean-field model (e.g., [Yokozawa, 1999](#); [Yokozawa and Hara, 1999](#)) as the patch model. This model is an IBM with assumptions A-I and A-II, in which the competitive effects of one plant on another plant are constant regardless of where these plants existed within a patch, and plants in one patch have no competitive effect on plants in different patches. The gap model is also an IBM with the same assumptions, while the size structure model is not ([Fig. 1](#)); however, size structure models can be easily transformed into the individual-based mean-field model without changing their parameters (see Appendix A in the Supplementary material for details). Therefore, we examined the parameter values and correction terms of not only the gap model but also the size structure models by using this IBM. The individual-based mean-field model clarifies the corresponding

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