Competition among plants can lead to an increase in aggregation of smaller plants around larger ones

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ABSTRACT

We re-examined traditional explanations regarding relationships between competition among plants and spatial patterns. We focused particularly on the prevailing view, which is that competition between smaller plants and larger plants serves only as a repulsive force between neighbors, and always decreases the degree of aggregation between smaller plants and larger plants over time. We propose an alternative underlying mechanism explaining the observed spatial patterns using a spatially explicit, individual-based model with general assumptions regarding the nature of competition among plants. We statistically estimated parameters for the model from observed census data collected over 30 years in an even-aged experimental fir forest (*Abies sachalinensis*). The results of our simulations, based on field data, indicated that asymmetric competition among plants led to the aggregation of smaller plants around a larger plant (i.e., not toward a uniform spatial pattern). This spatial pattern was generated by the growth suppression of plants near larger plants during the early growth stages, and more importantly, by the existence of a zone with lower competition intensity (referred to as competition-induced shelter, CiS) around a larger plant after the early growth stages. Larger plants compete for resources with large and medium-sized neighbors to the extent that the neighbors die and are removed, resulting in CiS. The results also indicate that competition between smaller plants and larger plants in an even-aged population exerts not only the traditionally recognized repulsive force but also a pseudo-attractive force, such as CiS, which promotes aggregation of smaller plants around a larger plant.

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1. Introduction

Plant ecological processes, such as competition, mortality, recruitment, and establishment, affect the spatial patterns of plants and *vice versa* (Watt, 1947; Greig-Smith, 1957; Ford and Diggle, 1981; Pacala and Deutschman, 1995; Dieckmann et al., 2000; Grabarnik and Särkkä, 2009, 2011). Thus, spatial patterns are closely related to the macroscopic aspects of plant populations and communities, including size structure (Bonan, 1988; Hara and Wyszomirski, 1994; Weiner et al., 2001), multi-species coexistence (Condit et al., 2000; Stoll and Prati, 2001; Murrell, 2009), vegetation succession (Smith and Goodman, 1987), ecosystem function in energy/matter flows (Pacala and Deutschman, 1995), and evolution (Yamamura et al., 2004). The aggregated spatial pattern of plants is of primary importance in this context because this type of spatial

pattern increases interactions among plants, resulting in intensive changes in macroscopic ecological aspects (Getzin et al., 2008).

Many studies have reported that the degree of aggregation of plants within the same size class (i.e., intra-size class) often decreases over time (Seiwa and Kikuzawa, 1987; He et al., 1997; Boyden et al., 2005). And, it has been also reported that the degree of aggregation of plants between different size classes (i.e., inter-size class) often decreases over time (Yeaton, 1979; Dovčiak et al., 2001). The development of less aggregated spatial pattern within a size class and between different size classes over time is thought to be due to self-thinning caused by intense competition for resources among neighboring plants (for example, Kenkel, 1988). Here, self-thinning (i.e., mortality due to competition) serves as a repulsive force, removing neighboring plants, which in turn increases the distance between the surviving plants and consequently reduces their degree of aggregation (for, example, Kenkel, 1988). Previous studies have reported that the degree of aggregation of plants around larger plants tend to become lower than that around smaller ones both within a size class (Seiwa and Kikuzawa, 1987; Moeur, 1997;

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Ward et al., 1996) and between size classes (Yeaton, 1979; Dovčiak et al., 2001) because larger plants exert a stronger repulsive force on their neighbors, with plants closer to the larger plant being more likely to die and be removed (Seiwa and Kikuzawa, 1987).

However, several studies have indicated that competition among plants does not always lead to a decrease in aggregation of plants. For example, Wyszomirski and Weiner (2009) showed that size-symmetric competition without mortality led to a positive correlation between plant size and the size of the neighboring plants as a consequence of the initial non-uniform spatial patterns of plants by growth suppression due to competition. Using models that incorporate both competition among neighbors and seed dispersal, some studies have shown that plants can be aggregated even when competition is intense (Bolker and Pacala, 1997; Law et al., 2003; Murrell, 2009); however, these theoretical studies did not show that competition alone could lead to the aggregation of plants. Previous studies have left the following question unanswered: does competition among plants always lead to a decrease in aggregation of plants (i.e., toward a uniform spatial pattern of plants)?

In this study, we revisited the traditional explanations regarding the relationship between competition among plants and spatial patterns, focusing particularly on the issue of whether competition between smaller plants and larger plants acts only as a repulsive force between neighbors, and whether the degree of aggregation between smaller plants and larger plants always decreases over time as a consequence of this function. We used an individual-based model that incorporated the following general assumptions regarding the nature of plant competition: (A_1) local crowding reduces plant growth and the probability of survival (Begon et al., 2005); (A_2) size is an important determinant of competitive ability (Keddy and Shipley, 1989; Weiner, 1984); (A_3) at close distances, the effect of a neighbor attenuates with distance (Weiner, 1982; Tyler and D'Antonio, 1995); (A_4) beyond a certain distance, plants have no detectable effect on one another (e.g., Dieckmann et al., 2000); and (A_5) competition among plants is usually size asymmetric (Schwinning and Weiner, 1998; Thomas and Weiner, 1989; Weiner, 1990). These assumptions have been demonstrated (e.g., Stoll and Weiner, 2000) and used in many studies (Schneider et al., 2006; Vogt et al., 2010). We conducted simulations to determine which type of spatial pattern was formed, and how, by competition among plants in an even-aged plant population.

2. Materials and methods

2.1. Models

2.1.1. Competition–growth model for plants

The model for describing growth and competition is a modification of the model proposed by Schneider et al. (2006). If the trunk diameter at breast height (*DBH*) is taken as plant size, then the temporal change in relative growth rate for each individual is governed by the following equations:

$$s_i = \ln(DBH_i) \tag{1}$$

$$\frac{ds_i}{dt} = \theta_1 - \theta_2 s_i - \theta_3 \sum_{j \neq i} F\left(\mathbf{x}_i, s_i; \mathbf{x}_j, s_j; \boldsymbol{\theta}\right) \tag{2}$$

where the index i (=1, ..., n) specifies a plant, and n is the total number of plants. The first term in Eq. (2), θ_1, represents the intrinsic growth rate due to uptake of resources. The second term, $\theta_2 s_i$, represents the metabolic loss, which is proportional to the natural logarithm of the size of an individual, DBH_i. We assumed here that the growth of each plant obeys the Gompertz model in situations with a non-competing population. The function $F(\mathbf{x}_i, s_i; \mathbf{x}_j, s_j; \boldsymbol{\theta})$ is the competition kernel (Law et al., 2001; Purves and Law, 2002;

Schneider et al., 2006), which represents the suppressive effect of a neighboring plant j of size s_j located at $\mathbf{x}_j$ on the growth of plant i of size s_i located at $\mathbf{x}_i$, where $\mathbf{x}_i$ and $\mathbf{x}_j$ are position vectors for plants i and j, respectively. The third term in Eq. (2) represents the reduction in the relative growth rate caused by competition among neighbors. The following function is referred to as competition intensity (*CI*):

$$CI\left(\mathbf{x}_i, s_i\right) = \sum_{j \neq i}^{n} F\left(\mathbf{x}_i, s_i; \mathbf{x}_j, s_j; \boldsymbol{\theta}\right) \tag{3}$$

It quantifies the degree to which a plant i suffers from competition due to other plants.

No information on the functional form of the competition kernel is available. We therefore considered seven possible candidates for the competition kernel function (Eqs. (4a)–(4g) in Table 1) and selected the best one according to model-selection criteria. The functional forms of the candidate kernel were devised by modifying the competition kernel functions following Schneider et al. (2006). The kernel functions in Table 1 show that the competition strength from neighboring plant j on target plant i depends at least on the size (s_i or DBH_i) of the target plant, the size (s_j or DBH_j) of the neighbor, and the distance d_{ij} (=$||\mathbf{x}_i - \mathbf{x}_j||$) between them. The effect increases as the size of plant j increases and decreases as the distance increases. The attenuation of competition with distance is described by hyperbolic-type (Eqs. (4a)–(4d) and (4g)) or Gaussian functions (Eqs. (4e) and (4f)). The parameter θ_4 included in the kernel functions describes how quickly competition strength attenuates.

We further assumed that each neighboring plant j has a circular zone of influence (ZOI), which is the novel and important point of our model compared to the original model proposed by Schneider et al. (2006). The suppressive effect of plant j on the growth of plant i disappears if plant i is outside the ZOI of plant j. If the ZOI is not included in the kernel function, then the θ parameter set could vary with the plot size because the effect of remote plants cannot be eliminated and it increases with the plot size. We assumed that the functional form determining the radius of the ZOI is exponential (Eqs. (4a), (4b), and (4e)) or logistic (Eqs. (4c), (4d), and (4f)). The radius of the ZOI in Eq. (4g) depends on the value of the competition kernel function F, and the competition strength gradually approaches zero with increasing d_{ij}. These functions depend on the size of a target plant and its neighbors as represented by *DBH* (Eqs. (4b) and (4d)) or the natural logarithm of *DBH* (s) (Eqs. (4a), (4c) and (4e)–(4g)). The degree of competitive asymmetry (Schwinning and Weiner, 1998; Thomas and Weiner, 1989; Weiner, 1990) is implemented as a parameter θ_5 in Eqs. (4a)–(4g). The degree of competitive asymmetry indicates the degree to which competition strength disproportionally increases with the increasing difference in size of two competing plants.

2.1.2. Mortality model for plants

The prediction of a binary response, such as the tree status "dead" or "alive," from continuous independent variables implies a logistic regression model (Hosmer and Lemeshow, 1989; McCullagh and Nelder, 1989; Collett, 1991). A distinct advantage of logistic regression models is that there are well-established procedures for model fitting and model testing (Collett, 1991). Logistic regression models have been used in many studies of the mortality of plants in forests (e.g., Bigler and Bugmann, 2004). In addition, here, we used competition intensity as the independent variable and did not consider other factors (e.g., age of plants) because the aim of this study was to examine the causal relationship between competition among plants and the spatial patterns