

## Development of a Local Size Hierarchy Causes Regular Spacing of Trees in an Even-aged *Abies* Forest: Analyses Using Spatial Autocorrelation and the Mark Correlation Function

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- **Background and Aims** During the development of an even-aged plant population, the spatial distribution of individuals often changes from a clumped pattern to a random or regular one. The development of local size hierarchies in an *Abies* forest was analysed for a period of 47 years following a large disturbance in 1959.
- **Methods** In 1980 all trees in an 8 × 8 m plot were mapped and their height growth after the disturbance was estimated. Their mortality and growth were then recorded at 1- to 4-year intervals between 1980 and 2006. Spatial distribution patterns of trees were analysed by the pair correlation function. Spatial correlations between tree heights were analysed with a spatial autocorrelation function and the mark correlation function. The mark correlation function was able to detect a local size hierarchy that could not be detected by the spatial autocorrelation function alone.
- **Key Results** The small-scale spatial distribution pattern of trees changed from clumped to slightly regular during the 47 years. Mortality occurred in a density-dependent manner, which resulted in regular spacing between trees after 1980. The spatial autocorrelation and mark correlation functions revealed the existence of tree patches consisting of large trees at the initial stage. Development of a local size hierarchy was detected within the first decade after the disturbance, although the spatial autocorrelation was not negative. Local size hierarchies that developed persisted until 2006, and the spatial autocorrelation became negative at later stages (after about 40 years).
- **Conclusions** This is the first study to detect local size hierarchies as a prelude to regular spacing using the mark correlation function. The results confirm that use of the mark correlation function together with the spatial autocorrelation function is an effective tool to analyse the development of a local size hierarchy of trees in a forest.

**Key words:** *Abies*, local size hierarchy, mark correlation function, pair correlation function, regenerating forest, regular spacing, spatial autocorrelation.

### INTRODUCTION

During the development of an even-aged plant population, the spatial distribution of individuals often changes from a clumped pattern to a random or regular one (Cooper, 1961; Ford and Diggle, 1981; Kenkel *et al.*, 1997; He and Duncan, 2000; Stoll and Bergius, 2005). This change in spatial distribution pattern is known as regular spacing. Regular spacing would be the result of density-dependent mortality, which is thought to be driven by asymmetric competition for light (Antonovics and Levin, 1980; Hutchings, 1997; Law *et al.*, 2001). During this process some individuals are suppressed by other, superior individuals, and the superior individuals are often surrounded by small trees, which results in the development of a 'local size hierarchy' of trees (Ford, 1975). In a population with a local size hierarchy, superior trees tend to be distributed regularly and mortality rates of suppressed trees are higher than those of superior trees, which produces a regularly spaced pattern of surviving trees.

The development of local size hierarchies in experimental herb populations has been detected by negative spatial autocorrelation between neighbouring individuals (Hozumi *et al.*, 1955; Yoda *et al.*, 1957; Ford and Renshaw, 1984; Franco and Harper, 1988). A negative spatial autocorrelation indicates

that there are large size differences between neighbouring individuals (i.e. large individuals are likely to be next to small ones and vice versa). Negative spatial autocorrelation as a result of such a local size hierarchy has also been observed in plantation and natural forests (Cooper, 1961; Reed and Burkhart, 1985; Liu and Burkhart, 1994; Mast and Veblen, 1999; Mast and Wolf, 2006).

Reed and Burkhart (1985) proposed that temporal changes in spatial autocorrelation of tree sizes in a plantation forest occur in the following manner: (1) in a young stand, variation in microsite conditions results in positive autocorrelation; (2) as the stand develops prior to self-thinning, spatial autocorrelation becomes negative as dominant trees suppress neighbouring trees (i.e. development of a local size hierarchy); and (3) mortality of small trees as the stand experiences self-thinning results in the development of positive autocorrelation. However, it is uncertain whether this process would be applicable to natural forests, because trees are distributed in random or clumped patterns. For instance, there could be extensive crowded areas in which a few dominant trees suppress a large number of smaller trees. In this case, the neighbours of large trees must be small trees, but the neighbours of small trees may be either large or small ones; accordingly, spatial autocorrelation would be neither positive nor negative. Indeed, some studies have failed to detect the expected

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negative spatial autocorrelation due to size hierarchies (Cooper, 1961; Kenkel *et al.*, 1997).

The functions used for detecting spatial autocorrelation of sizes, such as Geary's  $C$  or Moran's  $I$ , only indicate similarity between individuals at given distances. In contrast, the mark correlation function, an analysis of marked-point processes, can describe a multitude of sizes of individuals at given distances (Gavrikov and Stoyan, 1995; Stoyan and Penttinen, 2000; Illian *et al.*, 2008). The mark correlation function can elaborate the development of the local size hierarchy that cannot be detected by spatial autocorrelation functions alone. Thus, analyses using both the mark correlation and a spatial autocorrelation function can properly detect the development of a local size hierarchy.

This study aims to analyse the development of local size hierarchies followed by regular spacing using a spatial autocorrelation function and the mark correlation function in a subalpine *Abies* forest. After a large disturbance by a typhoon in 1959, the forest is still in the process of regenerating from saplings already established, rather than from seedlings that emerged after the disturbance (Kimura *et al.*, 1986). Regular spacing is expected to occur because of the patchy distribution pattern of *Abies* saplings (Kato and Yamamoto, 2001; Mori and Takeda, 2004a). Mortality would be higher within the *Abies* patches than outside because intense competition between trees after a canopy disturbance would be inevitable within the patches. In addition, a local size hierarchy is expected to have developed during the early stages of regeneration because of the great variation in size of the *Abies* saplings (Kimura *et al.*, 1986; Kato and Yamamoto, 2000, 2001). Under these circumstances, small saplings would be suppressed by large saplings immediately after canopy opening.

In this forest, we predicted the following: (1) a clumped distribution of saplings would become less clumped or regularly distributed as saplings grew; and (2) a local size hierarchy of saplings and trees would develop soon after the canopy opening.

## MATERIALS AND METHODS

### Study site

The study was conducted in a subalpine coniferous forest on Mt. Shimagare in the northern Yatsugatake Mountains in Japan (2100–2300 m a.s.l.). The annual mean temperature of the region is about 1.6 °C, and mean snow depth in winter is 1.0–1.5 m deep (National Land Agency of Japan, 1988). More than 1 km<sup>2</sup> of the forest was completely destroyed by the Isewan typhoon in 1959 and is now in the process of regenerating from a sapling bank. The dominant species of the forest are *Abies veitchii* and *A. mariesii* (Kimura, 1963; Kimura *et al.*, 1986).

### Field methods

In 1980, an 8 × 8 m plot was established at about 2230 m a.s.l. (36°4'N, 138°19'E; Kimura *et al.*, 1986). Positions of all trees in the plot were recorded as  $x$ - $y$  coordinates. Height growth between 1959 and 1980 of each *Abies* tree was estimated by the length between the branch whorls

on the trunk in 1980 (Kimura *et al.*, 1986). The heights of the leader shoots were measured in 1984, 1988, 1992 (Hara *et al.*, 1994), and every year from 1993 to 2006. Diameter at breast height (DBH) of trees taller than 1.3 m was measured in 1980, 1984, 1988, 1992, 1997 and 2004. The detailed measurement of growth trajectory restricted the plot size, but there were sufficient numbers of trees to analyse the spatial structure of the forest ( $n = 209$  in 1980).

Few trees died before the initial survey; there were ten standing dead trees in the plot in 1980 (Kimura *et al.*, 1986). Although some stems could have decayed before the survey, they would have been very small (Kimura *et al.*, 1986).

### Data analysis

Spatial distribution patterns of trees were analysed with the pair correlation function,  $g(r)$ . The function  $g(r)$  estimates how many trees are present at distance  $r$  around a tree and is normalized to equal 1.0 under a random distribution of trees (Penttinen *et al.*, 1992; Stoyan and Stoyan, 1994; Stoyan and Penttinen, 2000; Illian *et al.*, 2008). The value of  $g(r)$  is larger than 1.0 if the distribution pattern is clumped at a scale of distance  $r$ , and  $g(r)$  is smaller than 1.0 if the distribution pattern is regular at a scale of distance  $r$ . The pair correlation function is estimated by the following:

$$\hat{g}(r) = \frac{\sum_{ij} W(\|X_i - X_j\| - r)w(i, j)^{-1}}{2\pi n(n/ab)} \quad (1)$$

where  $n$  is the number of trees in the plot;  $a$  and  $b$  are the lengths and width of the plot, respectively;  $w(i, j) = ab - [ \|X_i - X_j\| (2a + 2b - \|X_i - X_j\|) / \pi ]$  is Ohser's edge-effect correction term;  $W(t) = 3/4\delta [1 - (t^2/\delta^2)]$  if  $|t| < \delta$ , and 0 otherwise (the Epanecnikov kernel), where  $\delta$  is the so-called bandwidth parameter. Stoyan and Stoyan (1994) recommended applying this parameter as  $\delta = c(nlab)^{-0.5}$ , where  $0.1 \leq c \leq 0.2$ . In this study,  $c$  was assumed to be 0.2 if  $c(nlab)^{-0.5} > r$ , otherwise  $c = r$ . The function  $\hat{g}(r)$  was calculated from  $r = 0.1$  to 4 m at 0.05-m intervals.

Spatial correlations between tree heights were analysed with the summary function  $\kappa_f = f(m_i, m_j)$  (Walder and Stoyan, 1996; Stoyan and Penttinen, 2000; Shimatani and Takahashi, 2003; Illian *et al.*, 2008), where  $f(m_i, m_j)$  is a so-called test function of marks (tree heights) of individuals  $i$  and  $j$  ( $m_i$  and  $m_j$ , respectively). For spatial autocorrelation,  $f_1(m_i, m_j) = 0.5(m_i - m_j)^2$  was used. The function  $\kappa_{f1}$  is called a mark variogram (Gavrikov and Stoyan, 1995; Walder and Stoyan, 1996; Stoyan and Penttinen, 2000; Illian *et al.*, 2008). If  $\kappa_{f1}$  is normalized using the following:

$$C(r) = \frac{\kappa_{f1}}{\sum (m_i - m_j)^2 / 2n(n-1)} \quad (2)$$

then  $C(r)$  is nearly equal to Geary's  $C$ , a standard function for spatial autocorrelation. For small  $r$ , when  $C(r) < 1$  neighbouring trees tend to have a similar height (i.e.

positive spatial autocorrelation), whereas  $C(r) > 1$  means that heights of nearby trees are not similar (i.e. negative spatial autocorrelation). Moran's  $I$ , another spatial autocorrelation statistic, was also calculated; there were no significant differences between results using the two statistics.

If  $f_2(m_i, m_j) = m_i m_j$  was used and  $\kappa_{f_2}$  is normalized as indicated,  $k_{mm}(r)$  is the mark correlation function:

$$k_{mm}(r) = \frac{\kappa_{f_2}}{\bar{m}^2} \quad (3)$$

where  $\bar{m}$  is the mean of marks (Penttinen *et al.*, 1992; Stoyan and Penttinen, 2000; Illian *et al.*, 2008). For small  $r$ , when  $k_{mm}(r) < 1$  neighbouring trees within distance  $r$  tend to be smaller than the mean height,  $\bar{m}$ , and when  $k_{mm}(r) > 1$  trees tend to be larger than the mean.

The estimator for  $C(r)$  and  $k_{mm}(r)$ ,  $\hat{C}(r)$  and  $\hat{k}_{mm}(r)$ , were obtained from the following estimator function (Illian *et al.*, 2008):

$$\hat{k}_f(r) = \frac{\sum_{i,j} W(\|X_i - X_j\| - r) f(m_i, m_j) w(i, j)^{-1}}{\sum_{i,j} W(\|X_i - X_j\| - r) w(i, j)^{-1}} \quad (4)$$

The  $\hat{C}(r)$  and  $\hat{k}_{mm}(r)$  were calculated from  $r = 0.1$  to 4 m at 0.05-m intervals.

Monte Carlo simulations were used to determine the significance of deviations from each null hypothesis (Diggle, 1983; Kenkel, 1988; Kenkel *et al.*, 1997; Nanami *et al.*, 2005; Illian *et al.*, 2008). The first null hypothesis tested was complete randomness in the spatial distribution of trees. In each simulation, the same number of randomly distributed points was generated as the number of observed trees in the plot, and the function  $\hat{g}(r)$  was calculated for these randomly distributed points. The 95 % confidence envelopes of  $\hat{g}(r)$  were estimated from 1000 simulations. For the spatial distribution patterns of trees after 1980, the random mortality hypothesis was also tested. The null hypothesis was that the spatial distribution of surviving/dead trees did not differ from the distribution that is expected if plant mortality occurred in a spatially random manner. In each simulation, the positions of trees living in a particular year were randomly assigned to the observed positions of live trees in 1980, and  $\hat{g}(r)$  was calculated for this randomly surviving population. The 95 % confidence envelopes of  $\hat{g}(r)$  were estimated from 1000 simulations.

For the spatial correlation between the tree heights, the null hypothesis was complete spatial independence of tree height distribution. This hypothesis was tested by using the random labelling test (Diggle, 1983; Nanami *et al.*, 2005). In each simulation, observed heights of all live trees in a year were assigned randomly to the observed positions of all live trees; that is, the size distribution of tree heights and the spatial distribution of trees did not change. For this randomly labelled population,  $\hat{C}(r)$  or  $\hat{k}_{mm}(r)$  was calculated. The 95 % confidence envelopes of  $\hat{C}(r)$  and  $\hat{k}_{mm}(r)$  were estimated from 1000 simulations each.

## RESULTS

### Spatial distribution pattern

The estimated pair correlation function,  $\hat{g}(r)$ , indicated that the spatial distribution pattern of trees changed from clumped to random during the 47 years after the devastation caused by the typhoon (Figs 1 and 2). In 1959 the spatial distribution of trees was strongly clumped at small distances (significant at distances 0.30–1.80 m,  $P < 0.05$ ; Fig. 2A). Between 1959 and 1970 the number of trees increased from 182 to 207 (Fig. 1A, B). In 1970 the clumped distribution pattern was still evident (significant at distances 0.3–1.2 m; Fig. 2B), although the values of  $\hat{g}(r)$  had decreased. Because there was no obvious recruitment or mortality of trees between 1970 and 1980, the distribution patterns did not change during that decade (Fig. 2C). After 1980 the spatial distribution patterns became less clumped and the number of trees decreased (from 208 in 1980 to 97 in 2006; Fig. 1C–F). In 1992 the distribution pattern tended to be slightly clumped at small distances ( $r < 1$  m) and was significantly regular at distances between 1.90 and 2.05 m (Fig. 2D). In 1999  $\hat{g}(r)$  was larger than 1.0 at distances around 1 m and smaller than 1.0 at distances around 2 m, although these patterns were not significant (Fig. 2E). The value of  $\hat{g}(r)$  decreased at distances smaller than 0.5 m in 2006, but without significance (Fig. 2F).

The tests of the random mortality hypothesis indicated that the regular spacing progressed after 1980. The  $\hat{g}(r)$  values were less than the lower confidence limit derived from the random mortality hypothesis at distances between 1.10 and 3.00 m in 1992, between 1.95 and 2.15 m in 1999, and at 0.25 m in 2006 (Fig. 2C–F).

### Spatial autocorrelation

Spatial autocorrelation of tree heights changed from positive to no correlation during the early stages of regeneration and from no correlation to negative during the late stages. In 1959 there was positive spatial autocorrelation at small distances [ $\hat{C}(r) < 1$  at  $r < 2.1$  m,  $P < 0.05$ ; Fig. 3A). Although the values of  $\hat{C}(r)$  increased markedly after 1959, there was significant positive spatial autocorrelation at 0.70–0.85 m and 1.20–1.50 m in 1970 (Fig. 3B). The values of  $\hat{C}(r)$  were significantly less than 1.0 at 1.35–1.45 m in 1980 and at 1.25–1.50 m in 1992 (Fig. 3C, D). After 1992 a negative autocorrelation developed at small distances ( $r < 0.5$  m), with  $\hat{C}(r)$  significantly greater than 1.0 at 0.05–0.10 m in 1999 (Fig. 3E). The values of  $\hat{C}(r)$  in 1999 were very similar to those in 2006, although no significant negative autocorrelation was observed (Fig. 3F). Positive autocorrelation was significant at distances between 1.75 and 2.10 and between 2.60 and 3.10 m in 2006.

### Mark correlation

The estimated mark correlation function of tree heights,  $\hat{k}_{mm}(r)$ , was larger than 1.0 during the initial stages, but values decreased at small distances within the first decade. In 1959  $\hat{k}_{mm}(r)$  was larger than 1.0 at all distances, and the largest values were observed at around 0.5 and 3 m

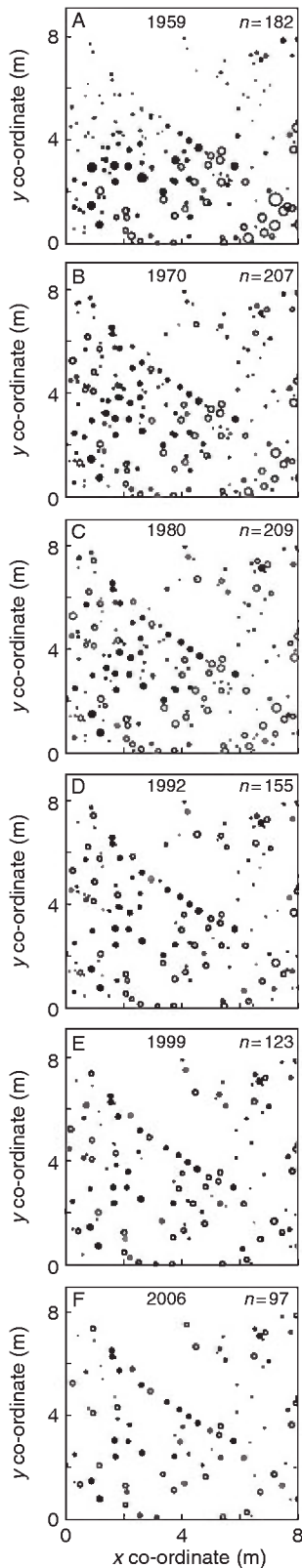


FIG. 1. Changes in the spatial distributions of living *Abies* trees at the study site during the period 1959–2006 (A–F). Open circles, positions of *Abies veitchii*; closed circles, positions of *A. mariesii*. The size of a circle represents the height of the tree relative to the mean height of all trees alive in the plot in each year.

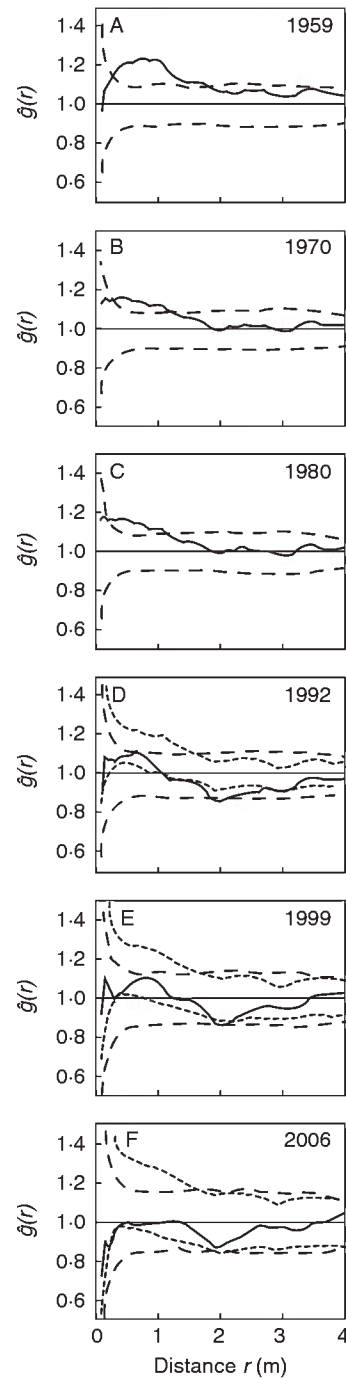


FIG. 2. Values of the pair correlation function,  $\hat{g}(r)$ , for living *Abies* trees during the period 1959–2006. The solid line shows observed  $\hat{g}(r)$  values, dashed lines show the 95 % confidence limits estimated from 1000 simulations based on complete spatial randomness, and dotted lines in (D–F) show the 95 % confidence limits estimated from 1000 simulations based on random mortality from 1980.

(significant at 0.30–1.05 m and 2.20–3.30 m; Fig. 3G). As the stand developed,  $\hat{k}_{mm}(r)$  values became smaller than those in 1959 at all distances. In particular, the values at distances smaller than 0.5 m decreased markedly in 1970 (significant at 0.05–0.15 m), and this trend was observed until 1999 (significant at 0.05–0.20 m in 1980,

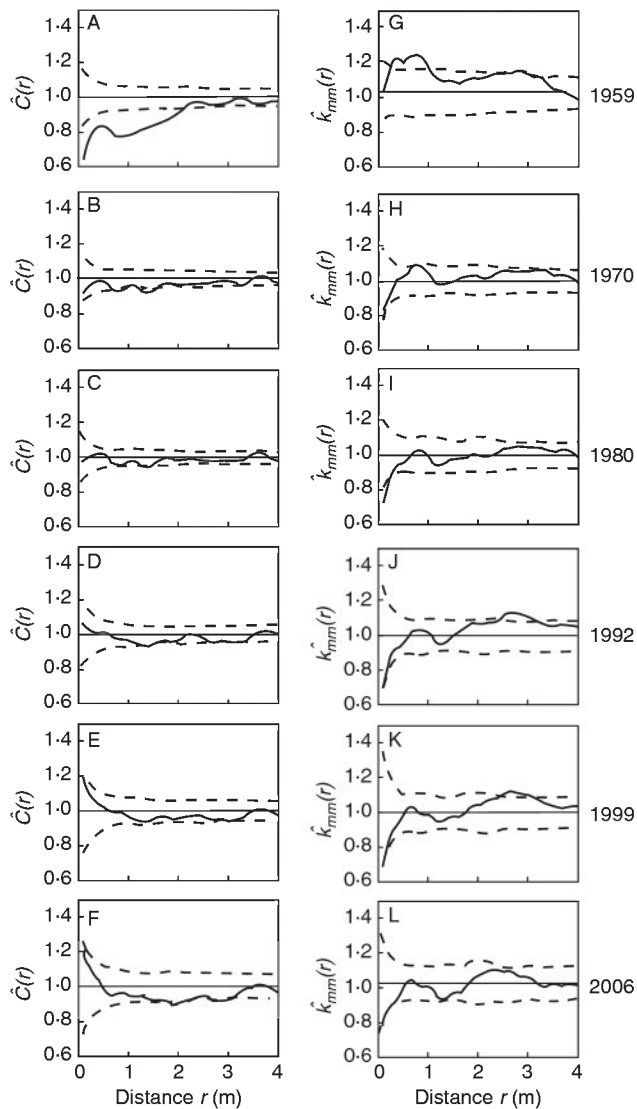


FIG. 3. (A–F) Values of the spatial autocorrelation statistic,  $\hat{C}(r)$ , and (G–L) the mark correlation function,  $\hat{k}_{mmm}(r)$  for living *Abies* trees during the period 1959–2006. The solid line shows observed  $\hat{C}(r)$  or  $\hat{k}_{mmm}(r)$  values, and the dashed lines show 95% confidence limits estimated from 1000 random labelling simulations.

0.05–0.15 m in 1992, 0.05–0.15 m in 1999; Fig. 3H–K). Between 1999 and 2006,  $\hat{k}_{mmm}(r)$  values at small distances increased slightly and did not significantly deviate from the 95% confidence limits. After 1992 the largest values were observed at distances around 3 m (significant at 2.45–3.15 m in 1992, 2.50–3.10 m in 1999, 2.55–2.70 m in 2006; Fig. 3J–L).

#### Simultaneous analyses of spatial autocorrelation and mark correlation

According to the simultaneous analyses of spatial autocorrelation and mark correlation, local size hierarchies developed during the first decade after the disturbance (Fig. 3A, G). In 1959 the spatial autocorrelation was positive

and the values of  $\hat{k}_{mmm}(r)$  were larger than 1 at distances around 1 m. That is, two trees with about 1 m distance between them were likely to have a similar large size, indicating that trees in a patch were more likely to be larger than those outside a patch. Large  $\hat{k}_{mmm}(r)$  for around  $r = 3$  m could indicate that the patches of large trees were distributed with a distance of approx. 3 m between them.

In 1970 there was no autocorrelation at distances smaller than 0.5 m, whereas  $\hat{k}_{mmm}(r)$  was less than 1.0 at these distances (Fig. 3B, H). Thus, neighbouring trees within 0.5 m of each other were small, on average, but the size variation was wide, indicating the development of a local size hierarchy. At this time, large trees were not close to other large trees, whereas small trees were close to small trees as well as large ones.

The increased values of the mark correlation and negative autocorrelation at small distances after 1999 (Fig. 3E, F, K, L) indicate that the number of small trees close to one another decreased. In this case, large trees had small neighbours and small trees had large neighbours, which could enhance development of a local size hierarchy. Small  $\hat{C}(r)$  and large  $\hat{k}_{mmm}(r)$  for around  $r = 3$  m at late stages indicate that trees with approx. 3-m distance between them would be a similarly large-sized.

## DISCUSSION

### *Spatial distribution pattern of trees*

Based on this investigation of a 47-year regeneration process, the analyses demonstrated that the development of a local size hierarchy is a prelude to regular spacing. Many studies have examined density-dependent mortality and regular spacing in plant populations (Cooper, 1961; Kenkel, 1988; He and Duncan, 2000; Stoll and Bergius, 2005), but their conclusions were derived from the significant spatial regularity of old forests or spatial patterns before and after mortalities. Although detailed maps have been presented for many tropical forests (Condit, 1995; Condit *et al.*, 1999; Hobbie, 2003), long-term processes of regular spacing have not been analysed together with the spatial association of tree sizes in these forests. Only one study has directly observed the processes that generate regular spacing and changes in spatial autocorrelation of tree sizes, namely Kenkel *et al.* (1997) who investigated the growth dynamics of a pine forest over 41 years. They did not detect any evidence for the development of local size hierarchies, however, possibly because their analysis with the spatial autocorrelation of tree sizes was not able to detect these hierarchies.

### *Spatial autocorrelation*

The positive spatial autocorrelation of tree sizes observed at the initial stage indicates that similar-sized trees existed as patches. These patches could have been produced because of variation in fine-scale light conditions on the forest floor before canopy opening. Light conditions could greatly affect the spatial distribution and sizes of saplings because *Abies* saplings are more likely to establish in less-

shaded places on the forest floor (Kohyama, 1983, 1984; Mori and Takeda, 2004a), where they become large (Mori and Takeda, 2003, 2004b). Thus, if less-shaded places were patchily distributed on the forest floor, there could be dense patches of large saplings at these places. It is likely that less-shaded places were patchily distributed at the study site before the disturbance because the site had been covered by a sparse forest of coniferous and deciduous species (Kimura *et al.*, 1986). This patchy distribution of favourable light conditions is consistent with the results from the mark correlation function, which indicated that trees in patches were more likely to be large than those outside a patch.

Negative spatial autocorrelation was detected only at the late stages (after 1992), when the number of living trees was less than half that in 1980. Although a local size hierarchy had developed by 1970, spatial autocorrelation was not negative because of the aggregation of small trees, as revealed by the mark correlation function. Only when some of the small aggregated trees died owing to suppression by canopy trees did spatial autocorrelation become negative, in 2006. This suggests that negative spatial autocorrelation occurs only if small trees are not aggregated under a local size hierarchy. Such cases would be rare in natural forests in which trees are distributed in a spatially random or clumped manner.

Reed and Burkhart (1985) predicted that positive autocorrelation of tree sizes would develop after self-thinning because of the high mortality of small trees. In the study plot, there were still some suppressed small trees even in 2006 (see Supplementary Information, available online). If those small trees die out, local size hierarchies would diminish and spatial autocorrelation would change from negative to less negative or positive.

#### Mark correlation function

The development of a local size hierarchy was successfully detected by the mark correlation function together with the spatial autocorrelation function. Therefore, in order to analyse the details of how local size hierarchies develop, the mark correlation function must be used in addition to use of the spatial autocorrelation. For this reason, development of local size hierarchy could be detected if the mark correlation function were to be applied for the previous studies that failed to detect it by the spatial autocorrelation alone (Cooper, 1961; Liu and Burkhart, 1994; Kenkel *et al.*, 1997; Mast and Veblen, 1999; Mast and Wolf, 2006).

In summary, this is the first attempt to detect local size hierarchies using the mark correlation function. Because development of a local size hierarchy is evidence of local competition and a prelude to regular spacing, the spatial autocorrelation function and the mark correlation function should be used together for a more comprehensive understanding of the regeneration process.

#### SUPPLEMENTARY INFORMATION

Supplementary material is available online at [www.aob.oxfordjournals.org/](http://www.aob.oxfordjournals.org/) and consists of a table giving a summary

of tree densities, basal area and height distribution statistics between 1959 and 2006, and a figure illustrating changes in the height distributions of *Abies* trees between 1959 and 2006.

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