



Tree mortality and habitat shifts in the regeneration trajectory underneath canopy of an old-growth subalpine forest

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ABSTRACT

To better understand tree regeneration trajectories and the resultant coexistence of *Abies* with co-dominants, *Picea jezoensis* var. *hondoensis*, *Tsuga diversifolia* and *Betula ermanii*, in an old-growth subalpine forest, we investigated spatial mortality patterns during the regeneration of *Abies mariesii* and *A. veitchii*, which are abundant in the understory reflecting their shade tolerance. Regeneration of these *Abies* spp. from shaded understory to canopy status is affected by other canopy co-dominants. Snags of understory *Abies* spp. were common, suggesting that the primary mortality agent is suppression by the overstory. Although live, small *Abies* trees in the understory were positively associated with a *Picea* canopy, the long-term survival was reduced among *Abies* trees close to the canopy, suggesting that shading by large *Picea* in the overstory negatively affects understory *Abies* plants. The existence of shade-intolerant canopy co-dominants such as *Picea* and also *Tsuga*, which are larger and longer lived than the shade-tolerant *Abies*, may play an important role in preventing the *Abies* spp. from competitively displacing these other tree species, which are much rarer in the understory, though common in the canopy. Moreover, in spite of the fact that *Betula* canopies fostered recruitment and growth of *Abies* saplings, *Abies* showed no association with *Betula* canopy and their survival at later-stage was rather reduced near or beneath *Betula* canopies at the subsequent understory small tree stage. Based on spatially significant events related to tree death, this study detected such “habitat shifts” in the trajectory of tree regeneration. Accordingly, it can be concluded that careful consideration of the regeneration habitat is required for a fuller understanding of ecological processes in spatially complex old-growth forest systems.

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1. Introduction

In old-growth forests, which are generally fairly stable in the absence of catastrophic disturbances (Spies, 2004), there is abundant potential for regeneration of trees, in spite of their suppressed status in the shaded understory (e.g. Lusk and Smith, 1998; Parent et al., 2003; Mori and Takeda, 2004a; Antos et al., 2005). Owing to their distinctive population characteristics, such as abundant advance regeneration and continuous size/age distribution, the shade-tolerant species in the understory are often believed capable of recruitment and continual growth without antecedent disturbances. Indeed, many old forests are characterized by a predominance of minimum-scale patch dynamics, whereby canopy turnover occurs mainly at the scale of a single tree fall (Lertzman, 1992; Veblen, 1992; Antos and

Parish, 2002; Mori and Takeda, 2004b; Worrall et al., 2005). This scale of tree-mortality events is regarded as a natural population-level process rather than as a disturbance because the event is not forced by an external perturbation (Łaska, 2001). Within such fairly “undisturbed” old-growth forests, life-history traits of late-successional, shade-tolerant species are important in explanations of population persistence under shaded conditions beneath relatively stable canopies (e.g. Antos et al., 2005). The prevalent view that continual regeneration accounts for persistence in these undisturbed forests is not acceptable. Mori et al. (2007) showed that two dominant conifers, *Abies mariesii* Masters and *Abies veitchii* Lindley, which are highly shade-tolerant (Kohyama, 1984, 1995; Mori and Takeda, 2003a, 2004c; Mori and Hasegawa, 2007), have limited recruitment and experience gradual population declines in a late-successional old-growth subalpine forest. Accordingly, it is important to determine the detailed regeneration trajectory of shade-tolerant tree species in old-growth forest systems from the strongly shaded understory to the sunlit canopy.

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Since tree mortality is a significant ecological process (Harmon et al., 1986; Franklin et al., 1987), description of mortality patterns beneath stable canopies is essential for an understanding of the regeneration dynamics of shade-tolerant species in old-growth forests (Lorimer et al., 2001; Hennon and McClellan, 2003; Busing, 2005). One example of a mortality pattern arising as a consequence of density-dependent competition is the frequent clustering of standing dead trees in smaller size classes (Parish et al., 1999; Rouvinen and Kuuluvainen, 2001); this spatial patterning of tree death affects the subsequent process of tree regeneration. Since old-growth forests are highly spatially heterogeneous both horizontally and vertically (Kneeshaw and Gauthier, 2003; Franklin and Van Pelt, 2004), events relating to the death and survival of regenerating trees may also be expected to vary spatially. Clarifying spatial patterns of mortality of shade-tolerant species before they reach canopy status will clearly contribute to an understanding of the regeneration dynamics in old-growth forests.

In the subalpine region of central Honshu, Japan, old forests are commonly characterized by the dominance and abundance of *A. mariesii* and *A. veitchii* (Franklin et al., 1979; Kohyama, 1995). Because these fir species are shorter-lived than other co-dominant genera, such as spruce (*Picea*) and hemlock (*Tsuga*) (Kanzaki, 1984; Miyadokoro et al., 2003), high recruitment of the firs in the understory, achieved through enhanced shade tolerance is an important demographic parameter that may compensate for their short life span (Mori and Takeda, 2004b). Similar demographic differences among species are often recognized as important components of coexistence mechanisms in many subalpine forests composed of such conifers (White et al., 1985; Veblen, 1986a,b; Antos and Parish, 2002). This recognition further emphasizes the need to clarify details of regeneration dynamics as components contributing to the demographic strategies of shade-tolerant *Abies* spp.

We focused on spatial patterns of mortality in *A. mariesii* and *A. veitchii* growing in an old-growth subalpine forest minimally affected by disturbances (Mori and Takeda, 2004b). Specifically, we asked whether there is a spatially specific habitat that favors or reduces plant survival in the regenerating stages of this old forest. Since favorable microsites (Wada and Ribbens, 1997; Coates, 2002; Mori and Takeda, 2004a), resource requirements (Poorter et al., 2005) and environmental conditions (Mori and Komiyama, 2008) are known to change as individual trees grow, we also asked whether such a mortality-related habitat would shift spatially as the life stages of the trees progressed.

2. Methods

2.1. Study site

This study was conducted in a subalpine old-growth forest (altitude 2050 m, 35°56'N, 137°28'E; WGS84) on Mt. Ontake (3067 m high) in central Honshu, Japan. This forest straddles two of the climatic regions on Honshu mainland (the rainy/snowy Sea of Japan side and the relatively dry/less-snowy Pacific Ocean side) (Franklin et al., 1979). Annual precipitation from 1984 to 2004, recorded near the study site, ranged from 1395 to 3607 mm, with an average of 2385 mm. Snow covers the forest floor from mid-November or early December to late May or early June, and maximum snow depths from 1995 through 2005 recorded near the study plot ranged from 165 to 240 cm. Average annual temperature is about 3–4 °C. The primary natural disturbances in this subalpine area are blowdowns, and large-scale canopy disturbances are caused occasionally by typhoons. Less-disturbed, late-seral forests are quite common. Very-small-scale canopy-patch dynamics predominate in these old forests.

The study forest consists mainly of four coniferous species: *A. mariesii* Masters, *A. veitchii* Lindley, *Picea jezoensis* var. *hondoensis* (Sieb. et Zucc.) Carrière and *Tsuga diversifolia* (Maxim.) Masters, all of which are thought to be representative species in many late-successional subalpine forests on the Honshu mainland. There is also a major hardwood species, *Betula ermanii* Cham., in the study forest. Although *Betula corylifolia* Regel et Maxim. also occurs, its frequency is lower than that of *B. ermanii*. On the whole, species composition of subalpine forests differs by regional climatic conditions on the Honshu mainland. Because of its geographical location and resultant climatic conditions, all representative conifer species on the Honshu mainland occur in the study forest. The detailed vegetational features of subalpine forests on Mt. Ontake have been described by Franklin et al. (1979). *Sasa*, the dwarf bamboo, which dominates the understory of many Japanese forests and interferes with growth of juvenile trees, was not present in the study plot.

2.2. Field methods

In May 2001, a 100 m × 90 m (0.9-ha) plot was established in a fairly undisturbed part of this subalpine forest (Mori and Takeda, 2004b). In 2002, this plot was extended to 100 m × 100 m (1.0 ha). For all live trees ≥ 2 m in height within the 1.0-ha plot, we measured the *x* and *y* coordinates and diameter at breast height (DBH; in cm), and recorded their position, size and species. For all dead trees ≥ 2 m in height (or ≥ 6 cm in diameter at ground level [DGL], if the stems were broken) within the 1.0-ha plot, we measured the *x* and *y* coordinates and DBH (or diameter of the highest point, if less than breast height) and recorded their position, size, species (or genus), type of death (snag or log) and decay class (from 1 to 5, as decay progresses; Antos and Parish, 2002). Some dead trees of *Abies* spp. and *Betula* spp. could not be identified to the species level because the bark was decomposed or missing. Therefore, they were referred to by their genus, i.e., *Abies* or *Betula*. Furthermore, dead trees of decay classes 4 and 5 were not even identifiable to the genus level and were classified as “unidentifiable” dead trees.

2.3. Data analyses

To analyze the spatial patterns of trees (height ≥ 2 m), univariate, bivariate and marked point-pattern analyses were conducted. All these analyses are useful in understanding spatial patterns of plant populations and for inferring their dynamics (e.g. Peterson and Squiers, 1995; Nanami et al., 1999; He and Duncan, 2000; Mori and Takeda, 2004b). The spatial pattern within each size class reflects the past process of regeneration (Lusk and Ogden, 1992). In these spatial analyses, all measured trees were classified into one of three life stages on the basis of criteria from Mori and Takeda (2004b), viz. small tree stage (DBH < 10 cm), subcanopy tree stage (10 cm ≤ DBH < 20 cm), and canopy tree stage (DBH ≥ 20 cm). For the two *Abies* spp., spatial statistics were computed for trees in each stage. For the other three major species, point-pattern analysis was done only for canopy trees, because there were no regenerating trees (Table 1).

The univariate spatial patterns of trees were analyzed using the function $L(t)$, the square-root transformation of Ripley's (1977) function $K(t)$ suggested by Besag (1977). $K(t)$ is defined as

$$K(t) = n^{-2}|A| \sum_{i \neq j} w_{ij}^{-1} I_t(u_{ij}) \quad (1)$$

where n is the number of plants in the plot; $|A|$ represents the area of plot; u_{ij} is the distance between two trees; w_{ij} is the proportion of the circumference of a circle with center at the i th tree and radius u_{ij} that lies within A ; $I_t(u)$ is equal to 1 if $u \leq 1$ and 0

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