Understory Herbaceous Species Composition Depends on Tree Canopy Dynamics in an Old-Growth Forest, Ogawa Forest Reserve, Northern Japan

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Introduction

Forest biota are adapted to and maintained by natural disturbance within the forest (e.g., Attiwill 1994). Therefore, it is often considered that one option for ecologically sustainable forest management is to emulate the intensity, frequency, and period of natural disturbance (e.g., Seymour and Hunter 1999; Lindenmayer and Franklin 2002; Mitchell et al. 2002; Crow and Perera 2004). Studies of the effects of natural disturbance in maintaining species diversity have increased in frequency (e.g., Nakashizuka 2001). In particular, canopy gap creation, a major source of natural disturbance in forest canopies and the focal point for consequent natural regeneration of trees, has been studied in relation to gap size (e.g., Abe et al. 1995; Vandenberghe et al. 2006) and microsites after gap creation (e.g., Carlton and Bazzaz 1998). However, most studies have only examined the responses of canopy dynamics of tall tree species and few have applied the results to forest management (e.g., Emborg et al. 2000).

The major source of natural disturbance in Ogawa Forest Reserve in northern Japan is canopy gap creation (Nakashizuka 2002). Therefore, when considering forest management practices to match the intensity, frequency, and period of canopy dynamics in the region, one should consider the understory species involved in the canopy dynamics. Species classification according to canopy dynamics has mainly focused on shade tolerance (e.g., Abe et al. 1995). However, to emulate natural disturbance in a target region forest management should focus on several species traits, not only shade-tolerance but also disturbance tolerance, because logging always involves physical disturbance to forest dynamics. Few studies have focused on species with tolerance to disturbance. Hence, in this study we evaluated species canopy dynamics in an old-growth forest in the Ogawa Forest Reserve with special reference to specific habitat types of species in the landscape.

Study site and methods

Study site

This study was conducted in the Ogawa Forest Reserve and the surrounding forested landscape, in Ibaraki Prefecture, northern Japan. The landscape consists mainly of deciduous broadleaf old-growth forests, coppice forests, and coniferous plantations. We conducted vegetation surveys in these three major forest types. For the deciduous broadleaf old-growth forest (hereafter, “old-growth”), we studied the Ogawa Forest Reserve and the reserved belt that maintains features of an old-growth forest (e.g., well-developed stand structure and large maximum stem size). In the coppice forest (hereafter, “coppice forest’), some stands were actively managed for fuel and firewood, but some, in particular stands 30 or more years old, had been abandoned. *Cryptomeria japonica*, an evergreen conifer and important commercial timber species in Japan, is planted in the coniferous plantations. The plantation stands sampled for this study (hereafter, “plantation”) had a wide age range and management intensity, indicating the diverse management aims and motivations of forest owners or managers. For example, weeding and thinning were carried out on schedule in some stands, while other stands were almost abandoned, without any management occurring after planting.

Plant survey

A plot (200 × 300 m) was established and divided into a 10 × 10-m grid in the Ogawa Forest Reserve. A 2 × 2-m quadrat was set up at the intersection of each grid (651 quadrats in total). Beside the Ogawa Forest Reserve, 43 stands (old-growth: 4; coppice forest: 13; and plantation: 26) were examined. A belt 10-m wide and 100-m long was established in each stand. To exclude the effects of different management types in neighboring stands, study plots were set up at the center of each stand, where possible. The belt-shaped plots were designed to cover topographic variations in each stand and thus minimize variation in natural conditions (e.g., slope aspect and soil type) among the stands (Iida & Nakashizuka 1995; Fukamachi et al. 1996; Nagaike et al. 2005). Basically, each coppice forest and plantation, except for those less than 10 years old, had not been managed for at least 5 years. Coppice forest and plantation stand age ranged from 1 to 77 and from 4 to 76 years, respectively. Each belt-shaped plot was divided into 5 × 5-m grids; a 1 × 1-m quadrat was placed at the corner of every 5 × 5-m grid square. To analyze the different quadrat sizes (i.e., 2 × 2 m in Ogawa Forest Reserve and 1 × 1 m in belt-shaped plots), we transformed the data of four 1 × 1 m plots into 2 × 2 m in the belt-shaped plots.

The total number of quadrats investigated was 1059 (old-growth: 691; coppice forest: 122; and plantation: 246). All herbaceous species, including ferns, less than 2-m tall occurring in each 1 × 1-m quadrat were recorded. The survey was carried out twice (1991 and 2001) in the Reserve and once from 2001 to 2004 in the other stands.

Canopy dynamics

In the Ogawa Forest Reserve plot, canopy height above each quadrat (for 651 quadrats) was measured with a measurement pole in 1989 and 2001. We classified the canopy height in each survey into three categories: “gap”: $\leq$10 m; “development”: <10 m to $\leq$ 15 m; and “closed”: >15 m. The canopy dynamics are shown comparing the height of the canopy in 1989 and 2001.

Analysis

Frequency of species occurrence was summed for each forest type (old-growth, coppice forest, and plantation). To delineate the habitat types for each species, the occurrence biases of species found in particular habitats were analyzed using chi-square tests, based on procedures in Nagaike et al. (2003, 2005). All species were divided into three habitat groups, according to whether they occurred disproportionately in the old-growth forest (Old-growth forest species), coppice forest (Coppice forest species), plantation (Plantation species), or were without bias to a particular forest type or too infrequent for statistical analysis (Other species). We also examined whether a species is considered to be a weed (Numata & Yoshizawa 2002).

Results and discussion

We recorded a total of 353 species: 208 in old-growth forest, 206 in coppice forest, and 246 in the plantation. Of these 353 species, Other species (249 species, e.g., *Blechnum niponicum*, *Carex fernaldiana*, and *Smilax sieboldii*) made up the highest proportion, followed by Old-growth forest species (57 species, e.g., *Ainsliaea acerifolia* var. *subapoda*, *Pertya robusta*, and *Pseudostellaria palibiniana*). Coppice forest species and Plantation species accounted for 23 (e.g., *Carex lanceolata*, *Viola grypoceras*, and *Ixeridium dentatum*) and 24 (e.g., *Athyrium yokoscense*, *Deparia conilii*, and *Bidens frondosa*) species, respectively. The ratio of weed species to the number of species of each forest type was highest for Coppice forest (52%), followed by Plantation (38%), and Old-growth forest (16%).

In old-growth forest, “closed” canopy increased in frequency from 569 quadrats in 1989 to 596 quadrats in 2001. Consequently, both “development” and “gap” canopy types decreased in frequency (from 41 to 33 “development” quadrats and from 41 to 22 “gap” quadrats). In quadrats where “gap” changed to “closed” (i.e., gap closure) from 1989 to 2001, newly-occurring species were mainly Old-growth forest species (eight of 14 species). Lost species in the quadrats constituted 17 species, mostly Old-growth forest species (eight species). In quadrats where “closed” changed to “gap” (i.e., canopy gap creation), there were 14 newly-occurring species, of which eight were Old-growth forest species (Table 1). Four of the eight lost species were Old-growth forest species.

Fewer weed species, which were expected to be tolerant to severe disturbance, were found in old-growth forest, and more were found in coppice forest and plantations. This indicates that coppice forest and plantations suffered more severe disturbance than old-growth forest. Species that were new or that had disappeared from gap-created and canopy-closure quadrats were mainly Old-growth forest species. Therefore, we concluded that species adapted to old-growth forest canopy dynamics were native to old-growth forest, but differed from species which occurred after severe disturbance (i.e., Coppice forest and Plantation species). Consequently, we need to establish forest management procedures that maintain the diversity of Old-growth forest understory species.

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Table 1. The responses of plant species to changes in canopy dynamics in the Ogawa Forest Reserve

	From “gap” to close”		From “close” to “gap”	
Species types	Newly occurred species	Disappeared species	Newly occurred species	Disappeared species
Old-growth forest species	8	8	8	4
Coppice forest species	1		1	1
Plantation species		3	3	
Others	5	6	3	3
Total	14	17	14	8