Changes in Plant Diversity after Conversion from Secondary Broadleaf Forest to *Cryptomeria* Plantation Forest: Chronosequencial Changes in Forest Floor Plant Diversity

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Introduction

The conservation of forest biological diversity is considered one of the most important criteria for ecologically sustainable forest management (Hunter 1999, Lindenmayer and Franklin 2002) because biological diversity is thought to be related to many ecological functions (Scherer-Lorenzen et al. 2005). This idea is still an open question. In addition to studies that focus on the relationships between biological diversity and ecological function, further information is required on the actual biological diversity of forested landscapes.

Conversions from primary broadleaf forests, coppice broadleaf forests, and semi-natural grasslands to conifer (sugi, *Cryptomeria japonica*, and hinoki, *Chamaecyparis obtusa*) plantations occurred after the 1940s in the mountainous areas of Japan, resulting in the replacement of a large portion of the natural and semi-natural vegetation of Japan by conifer plantations prior to the 1980s (Inoue 2003). Biological diversity sustained by traditional land use may have been negatively affected by the conversion of mixed stands to pure monocultures. Several studies have described the effects of such conversions on plant diversity in different regions and plantation forest types at the stand level (Nagaike 2002, Ito et al. 2003, 2004, Nagaike et al. 2005). However, few studies have investigated the dynamic chronosequential changes in plant diversity in both natural secondary forests and converted plantation forests (Nagaike 2003, Nagaike et al. 2006).

To sustainably manage a mosaic forest landscape composed of secondary broadleaf forests and conifer plantations, it is important to understand the plant diversity and how it changes with stand age of both forest types, as well as the contribution of each forest type to the maintenance of regional biodiversity. The appropriate zoning or spatial arrangement of stands for sustainable forest management depends on an understanding of the compositional characteristics of each forest type and age, as well as the dependence of plant species on forest type and age.

To obtain a scientific basis for plant diversity management and conservation, we addressed the following two specific questions. How does plant diversity change (recover) in both plantation and secondary natural forest stands after clear-cutting? How does conversion from deciduous broadleaf forest to evergreen conifer plantation affect species diversity? We used a chronosequence

approach to compare sample stands of different ages scattered across a typical landscape.

Materials and methods

Study sites

The study was conducted in two areas located about 10 km apart: Ogawa and Satomi, Ibaraki Prefecture, central Japan. Both areas are located at the southern edge of the Abukuma Mountains (approximately 36º 50–56′ N, 140º 34–35′ E; 580–800 m above sea level). The annual mean temperature and precipitation in Ogawa are 10.7ºC and 1910 mm, respectively (Mizoguchi et al. 2002). The landscape of both areas is now mainly composed of deciduous broadleaf forests and plantations of *Cryptomeria japonica* (partly of *Chamaecyparis obtusa*), although the proportion of plantations is much higher in Satomi than in Ogawa (94% vs. 47% of the total forested area, respectively). In old-growth broadleaf forests, which are preserved only in Ogawa, the dominant canopy trees are *Quercus serrata*, *Fagus japonica*, and *F. crenata* (Masaki et al. 1992, Tanaka et al. in press). A large portion of the broadleaf forests in Ogawa, including the old-growth forests, has long been subjected to human activities such as burning, cattle grazing, and clear-cutting for fuel (Suzuki 2002). Small-scale (1–2 ha) clear-cutting with short intervals of ca. 30 years has been conducted repeatedly until now in the secondary broadleaf forests to make charcoal, produce pulp wood, and collect bed logs for mushroom culture. The conversion of pasture or secondary broadleaf stands to conifer plantations greatly increased the proportion of plantation forests in Japan after the Second World War (Inoue 2003). In addition, this land-use history resulted in a mosaic-like forest landscape in these areas, composed of secondary broadleaf stands and conifer plantations of various ages.

Field study

We examined the forest vegetation in 13 post-harvest secondary deciduous broadleaf forests (SB) and 26 conifer (*Cryptomeria japonica*) plantation forests (CP) along a chronosequence from just after clear-cutting to mature stands (70–80 years old). Four preserved old deciduous broadleaf forests (OG) were also studied as a reference for old-growth conditions. Plantation forests had been tended (i.e., weeded and thinned) according to the common schedule of the local governmental forest offices, but not so intensively managed as well-managed private plantations.

  In each forest, we established a 10 × 100 m belt-shaped study plot at the center of each stand wherever possible to exclude the effects of neighboring stands of different management types. To minimize the influence of variation in site conditions, we selected stands located on gentle slopes, and the belt-shaped plots were designed to encompass the topographic variation in each stand (Iida and Nakashizuka 1995, Fukamachi et al. 1996, Nagaike 2002, Nagaike et al. 2003, 2006).

  Each study plot was divided into 5 × 5 m quadrats, and a 1 × 1 m subquadrat was positioned in the corner of each quadrat. In total, we investigated 1060 quadrats and subquadrats:

160 in old-growth forests, 380 in secondary forests, and 520 in plantation forests. In each study plot, trees and woody vines > 2 m in height and with a diameter at breast height (dbh) > 5 cm were tagged, and their girth at breast height (gbh) was measured. Forest floor vegetation, i.e., < 2 m in height, was censused within each subquadrat using the Braun-Blanquet method. Standing dead stems > 5 cm in dbh were tagged and measured. We also recorded all woody plants > 2 m in height in each quadrat. Light conditions at the forest floor were measured in each subquadrat using hemispherical photographs taken 1 m above the ground.

A 200 × 300 m plot was established in the Ogawa Forest Reserve, and 2 × 2 m quadrats were placed at each intersection of a 10 × 10 m grid (651 quadrats in total) for the collection of additional data on forest floor vegetation in old-growth forests. The nomenclature follows Kitamura and Okamoto (1959), Kitamura et al. (1974, 1978), and Kitamura and Murata (1980).

Data analysis

To define understory vegetation species groups, the occurrence biases of species found in particular forests were tested using chi-square and Fisher's exact tests, based on the procedure of Nagaike et al. (2003). To include the vegetation data from the Ogawa Forest Reserve 2 × 2 m quadrats, we analyzed the pooled data from four 1 × 1 m subquadrats. In total, we investigated 1059 2 × 2 m subquadrats (691 in old-growth forests, 122 in secondary forests, and 246 in plantation forests) from four old-growth forests, 13 secondary broadleaf forests, and 26 plantation forests. We examined whether species occurred disproportionately in old-growth forests, secondary forests, or plantations. Species with no significant bias were classified as generalists, whereas those with occurrence frequencies ≤ 5 were classified as infrequent species. Thus, species were classified into five types according to their occurrence bias toward particular forest types. In addition, we classified the species listed in Numata and Yoshizawa (2002) as weed species, which are characterized as ruderal or disturbance-tolerant species (Bhuju and Ohsawa 1999, Kitazawa and Ohsawa 2002) and are usually considered undesirable from a management perspective. Species listed in the Red Data Book (Environment Agency of Japan 2000) did not occur in the study area.

To examine the differences between secondary forests and plantation forests in forest floor plant species abundance, analysis of variance (ANOVA) was performed for stands pooled into three age categories: young (3–10 years old), intermediate (10–40 years old), and mature (≥ 41 years old) stands (JMP, SAS Institute 2001). To test for compositional differences among forest types, cluster analysis and detrended correspondence analysis (DCA) were performed using PC-ORD (McCune and Mefford 1999). The species occurrence frequency in each plot was used for DCA. Correlations between the axis scores of DCA and stand structural and compositional variables reflecting management intensity were calculated using Kendall's τ (JMP, SAS Institute. 2001).

Results
Changes in stand structure and species diversity with stand age

As stand age increased, stand structural parameters such as basal area (BA) increased in both secondary forests and conifer plantations (Fig. 1). The BA was larger in plantation forests than in secondary forests (and old-growth forests) along the chronosequence (Fig. 1), although the maximum dbh was comparable in secondary forests and conifer plantations (data not shown).

Young stands (2–10 years after clear-cutting) had higher species richness of forest floor plant species (i.e., herbs and ferns) than did intermediate (11-40 years) and mature stands (>40 years) in both secondary and plantation forests (Tukey-Kramer's HSD, $p < 0.01$; Fig. 2). The species richness of forest floor plant species was marginally higher in secondary forests than in plantation forests at each age category (ANOVA, $p = 0.05$; Fig. 2).
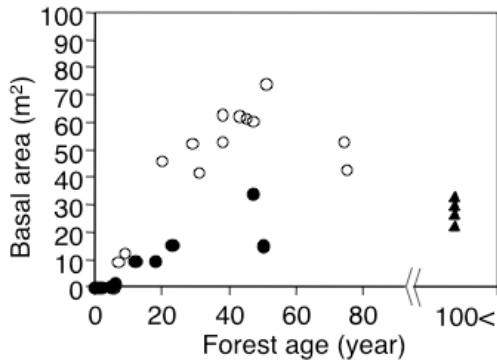

Fig. 1. Relationship between stand age and basal area (BA) of trees with diameter at breast height (dbh) > 5 cm. Open circle: conifer plantation; closed circle: secondary
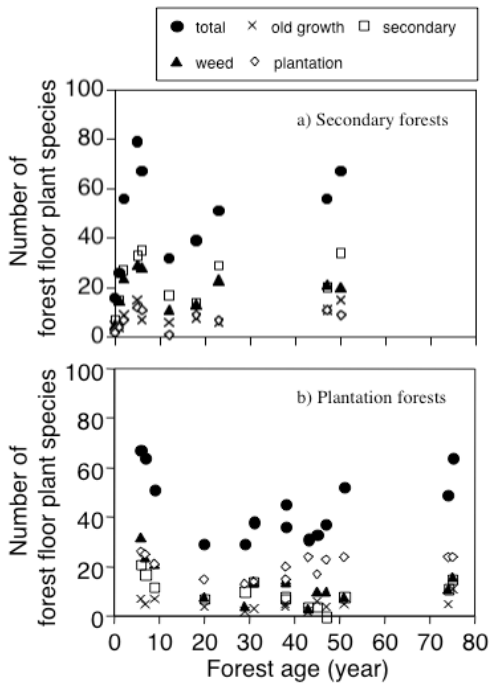
Fig. 2. Relationship between forest stand age and number of forest floor plant species in (a) secondary forests and (b) plantation forests.

Species diversity and composition in plantations and secondary forests

We recorded a total of 324 species (Fig. 3, Table 1). The three forest types appeared to contribute equally to the forest flora, although this result is based on restricted sampling (Fig. 3). According to the species occurrence biases, infrequent species (124 species, 38%) made up the highest percentage of species (Table 1). Secondary forest species (71 species, 22%) accounted for the second highest occurrence frequency, but plantation forest species accounted for nearly the same percentage (62 species, 19%). The secondary forest species group contained the highest percentage of weed species (41%). The old-growth forest species group contained the fewest weed species, but this was still a substantial percentage of the total species count (33 species, 10%).
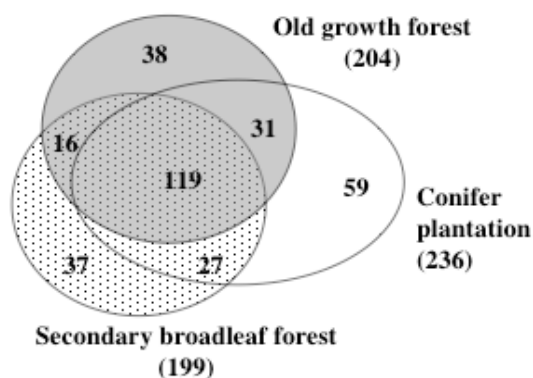

**Fig. 3.** Number of forest floor plant species in each forest type.

Table 1. Species groups classified with the distributional bias to the specific forest types.

Species group	No. of species	No. of weedy species (%)	Species
Old growth forest species	33	6 (18)	*Ainsliaea acerifolia* var. *subapoda, Pseudostellaria palibiniana, Salvia nipponica, Cynanchum magnificum, Viola eizanensis, Prenanthes acerifolia*
Secondary forest species	71	29 (41)	*Disporum smilacinum, Viola grypoceras, Hosta albo-marginata, Viola rossii, Luzula plumosa* var. *macrocarpa, Ixeris dentata, Carex lanceolata, Potentilla freyniana*
Plantation forest species	62	20 (32)	*Athyrium yokoscense, Oplismenus undulatifolius, Deparia conilii, Chloranthus serratus, Impatiens textori, Laportea bulbifera, Disporum sessile, Arachniodes borealis*
Others	158	39 (25)	
Common	34	7 (21)	*Carex sachalinensis* var. *alterniflora, Tricyrtis affinis, Elatostema umbellatum* var. *majus, Carex dolichostachya* var. *glaberrima, Arisaema serratum, Smilacina japonica, Cacalia farfaraefolia, Stellaria sessiliflora*
Infrequent species	124	32 (26)	*Caulophyllum robustum, Tulotis ussuriensis, Goodyera schlechtendaliana, Allium monanthum, Polygonatum involucratum, Chelidonium majus* var. *asiaticum, Scrophularia kakudensis*
Total	324	94 (29)	

Broadleaf (secondary and old-growth) and plantation forests were clearly distinguished by cluster analysis according to the forest floor plant species composition, although the difference between secondary forests and old-growth forests was not very distinct (Fig. 4). Broadleaf forests (secondary and old-growth forests) were also distinguished from plantation forests along axis 1 of the DCA ordination (Fig. 5). In addition, old-growth forests were distinguished from secondary forests along axis 2 (Fig. 5). According to the correlations between the DCA axis scores and forest age (Table 2), axis 2 was significantly positively correlated with forest age for both confer plantations and secondary forests. This is consistent with the placement of old-growth forests above secondary forests in the DCA ordination diagram (Fig. 2). For the plantation forests, the axis 1 scores were positively correlated with the proportion of plantation forest species and negatively correlated with the proportion of secondary forest species (Table 2). The axis 1 scores for secondary forests were negatively correlated with the proportion of secondary forest species (Table 2). The proportion of weed species was negatively correlated with axis 1 for secondary forests and axis 2 for plantation forests (Kendall's rank correlation, $p < 0.05$, Table 2).
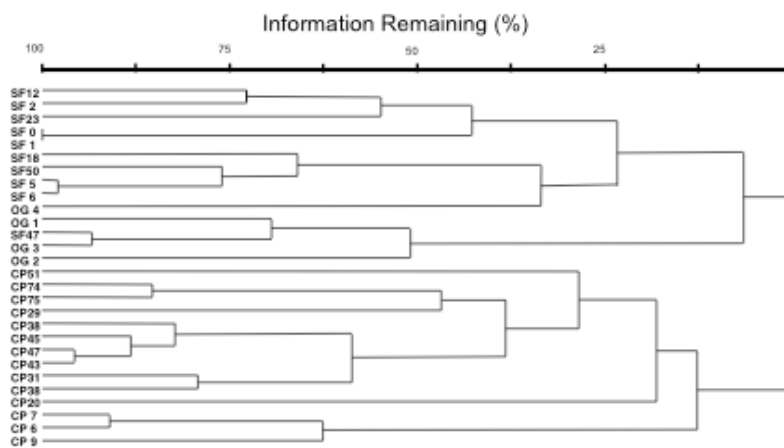
Fig. 4. Dendrogram showing the result of cluster analysis. Number in stand name indicates stand age.
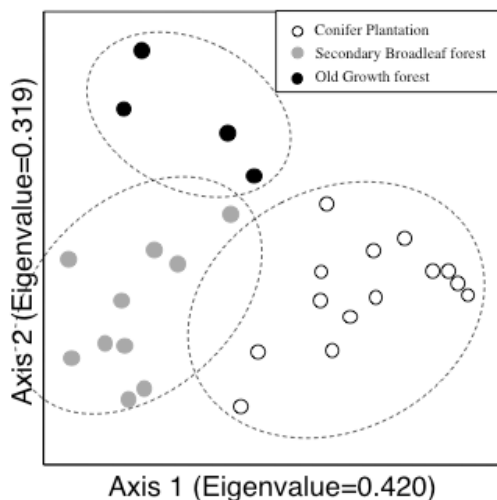
Fig. 5. Diagram of the results of detrended correspondence analysis (DCA). Each symbol indicates a stand.

Table 2. Correlation between the two axes of DCA and the forest age and the proportion of each species group (Kendall's rank correlation coefficient).

	Forest age	Proportion of old growth forest species	Proportion of secondary forest species	Proportion of plantation forest species	Proportion of weed species
Conifer plantation					
Axis 1	0.287	-0.022	-0.539**	0.473*	-0.275
Axis 2	0.729**	0.155	-0.407*	0.385	-0.495*
Secondary broadleaf forest					
Axis 1	0.500	0.389	-0.611*	0.222	-0.556*
Axis 2	0.556*	0.556*	-0.444	0.278	-0.389

*: $p < 0.05$, **: $p < 0.01$. †: marginally significant.

Ecological attributes of species in plantations and secondary forests

The proportion of weedy species was negatively correlated with stand age in both plantation and secondary forests ($\tau b = -0.500$, $p = 0.061$ for secondary forests; $\tau b = -0.464$, $p = 0.021$ for plantation forests; Fig. 6). The number of weedy species was highest approximately 5 years after clear-cutting in both secondary forests and plantation forests (Fig. 2). The proportion of secondary forest species was negatively correlated with stand age in plantation forests ($\tau b = -0.420$, $p = 0.037$; Fig. 6). The proportion of plantation forest species showed no significant correlation with stand age in either of the forest types (Fig. 6). The proportion of old-growth forest species showed a marginally positive correlation with stand age in secondary forests ($\tau b = 0.444$, $p = 0.095$; Fig. 6).
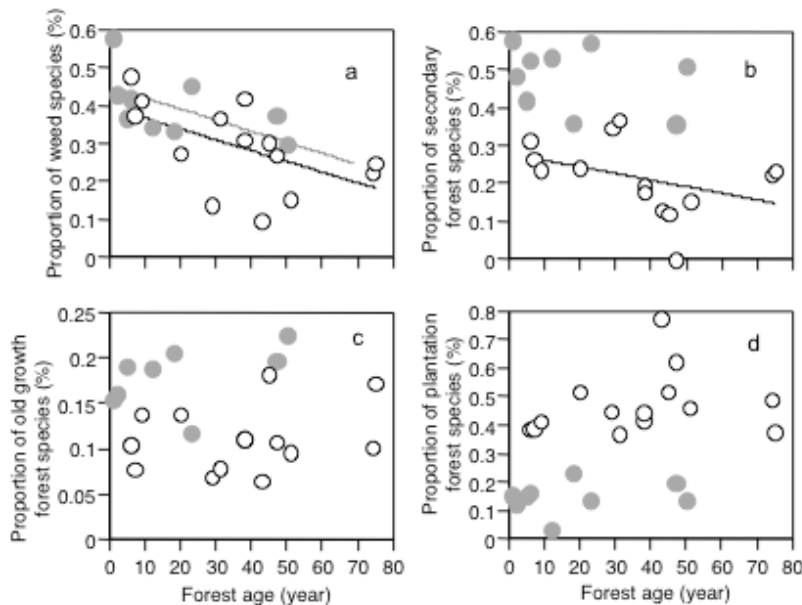
Fig. 6. Relationship between forest stand age and the proportion of four species types: (a) weed species, (b) secondary forest species, (c) old-growth forest species, and (d) plantation forest species.

Discussion

Although species richness differed only marginally between secondary and plantation forests along a chronosequence after clear-cutting and showed similar patterns of change along the chronosequence (Fig. 2), the conversion from secondary forests to plantation forests resulted in a distinctly different forest floor plant species composition (Figs. 4, 5). This difference is understandable because the conversion from deciduous broadleaf forest to evergreen conifer forest results in different microenvironments according to changes in canopy leaf composition and phenology (Ramovs and Roberts 2003). After canopy closure (ca. 10 years after clear-cutting), seasonal light, temperature, and moisture conditions are likely to be more temporally stable and spatially homogeneous in plantation forests than in secondary forests. Larger stem basal area in plantation forests relative to secondary forests (Fig. 1) may also contribute to the differences in forest floor microenvironments.

In both secondary forests and plantation forests, weeds accounted for a high percentage of species, suggesting the influence of severe disturbance; i.e., clear-cutting, in both forest types. The rather high percentage of weed species also found in old-growth forests may reflect the influence of large-scale disturbances, e.g., fire and grazing by horses and cattle, that frequently occurred in the past in this region (Suzuki 2002, Miyamoto and Sano 2007). The proportion of weed species decreased with stand age (time since disturbance) in both secondary and plantation forests (Fig. 6, Table 2). Colonization by a large number of weed species partly explained the high species diversity after clear-cutting (Fig. 2; Fahy and Gormally 1998, Bhuju and Ohsawa 1999, Nagaike 2000). Higher species richness in intensely managed stands has also been reported in many types of managed forest (Schoonmaker and McKee 1988, Brunet et al. 1996, Stapanian et al. 1998, Scherer et al. 2000).

Although the number and proportion of weed species decreased with stand age in both secondary and plantation forests, the results of DCA ordination and the relationships between the DCA axes and forest age suggest that the compositions of these forest types were not converging as stand age increased (Fig. 5). The proportion of secondary forest species in plantation forests decreased with stand age (Fig. 6). In contrast, the proportion of old-growth forest species did not change as stand age increased, even in secondary forests, suggesting that in the first 60 years post-clear-cutting in secondary that the abandonment of secondary coppice forests does not directly lead to the recovery of old-growth forest plant species (Ramovs and Roberts 2003). Thus, the preservation of the remaining old-growth forests is very important for the conservation of regional plant species diversity.

Relative to old-growth forests, both secondary forests and conifer plantations contributed substantially to local plant species diversity, although both contained large percentages of weed species (Fig. 3, Table 1). The plantation species included an abundance of ferns that may have taken advantage of the preferable environmental conditions of plantation forests (Table 1). Among the infrequent species, orchids were also found in plantation forests (Table 1). In contrast, most of the

spring ephemerals such as *Erythronium japonicum* and *Anemone pseudo-altaica* were only found in deciduous broadleaf forests (secondary and old-growth forests). Plantation forests may contribute to local plant diversity, but cannot substitute for secondary and old-growth forests (Maeto et al. 2002, Inoue 2003).

  To quantitatively evaluate the contribution of conifer plantations and secondary forests of different ages to the maintenance of local plant diversity, further understanding of the processes and mechanisms shaping species composition is necessary (Halpern 1989, Roberts and Gilliam 1995). In addition to the occurrence bias of forest floor plant species, information on the functional types (e.g., growth form, dispersal type, pollination type; Smith et al. 1997) of the component species will be important in understanding these processes and mechanisms.

References

Brunet J, Falkengren-Grerup U, Tyler G (1996) Herb layer vegetation of south Swedish beech and oak forests — effects of management and soil acidity during one decade. For Ecol Manage 88: 259–272

Bhuju D R, Ohsawa M (1999) Species dynamics and colonization patterns in an abandoned forest in an urban landscape. Ecol Res 14: 139–153

Environmental Agency of Japan (2000) Threatened wildlife of Japan—Red Data Book. Vascular plants. 2nd ed. Japan Wildlife Research Center, Tokyo.

Fahy O, Gormally M (1998) A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. For Ecol Manage 110: 263–273

Fukamachi K, Iida S, Nakashizuka T (1996) Landscape patterns and plant species diversity of forest reserves in the Kanto region, Japan. Pl Ecol 124: 107–114

Halpern C B (1989) Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology 70: 704–720

Hunter Jr, M L ed (1999) Maintaining biodiversity in forest ecosystems. Cambridge University Press, Cambridge

Iida S, Nakashizuka T (1995) Forest fragmentation and its effect on species diversity in sub-urban coppice forests in Japan. For Ecol Manage 73: 197–210

Inoue T (2003) Chronosequential change in a butterfly community after clear-cutting of deciduous forests in a cool temperate region of central Japan. Entomol. Sci. 6: 151–163

Ito S, Nakagawa M, Buckley G P, Nogami K (2003) Species richness in sugi (Cryptomeria japonica D. Don) plantations in southeastern Kyushu, Japan: The effects of stand type and age on understory trees and shrubs. J For Res 8: 49–57

Ito S, Nakayama R, Buckley G P (2004) Effects of previous land-use on plant species diversity in semi-natural and plantation forests in a warm-temperate region in southeastern Kyushu, Japan. For Ecol Manage196: 213–225

Kitamura S, Murata G (1980) Colored illustrations of herbaceous plants of Japan (Choripetalae). Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitamura S, Murata G, Hori M (1978) Colored illustrations of herbaceous plants of Japan (Sympetalae).

Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitamura S, Murata G, Koyama T (1974) Colored illustrations of herbaceous plants of Japan (Monocotyledoneae). Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitamura S, Okamoto S (1959) Colored illustrations of trees and shrubs of Japan. Hoikusya Publishing Co. Ltd., Osaka, Japan. [In Japanese.]

Kitazawa T, Ohsawa M (2002) Patterns of species diversity in rural herbaceous communities under different management regimes, Chiba, central Japan. Biol Conserv 104: 239–249

Lindenmayer D B, Franklin J F (2002) Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington, D.C.

Maeto K, Sato S, Miyata H (2002) Species diversity of longicorn beetles in humid warm-temperate forests: the impact of forest management practices on old-growth forest species in southwestern Japan. Biodiv Conserv 11: 1919–1937.

Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H, Nakashizuka T (1992) Community structure of a species rich temperate forest, Ogawa Forest Reserve, central Japan. Vegetatio 98: 97–111

McCune B, Mefford M J (1999) PC-ORD: multivariate analysis of ecological data; version 4 [computer program]. MjM Software Design, Gleneden Beach, Oregon.

Miyamoto A, Sano M (2007) The influence of change in forest resource use on forest landscapes in Abukuma mountainous area in the past 90 years. this volume.

Mizoguchi Y, Morisawa T, Ohtani Y (2002) Climate in Ogawa Forest Reserve. Ecol studies 158: 11–18.

Nagaike T (2002) Differences in plant species diversity between conifer (Larix kaempferi) plantations and broad-leaved (*Quercus crispula*) secondary forests in central Japan. For Ecol Manage 168 (1): 111–123

Nagaike T, Hayashi A, Abe M, Arai N (2003) Differences in plant species diversity in *Larix kaempferi* plantations of different ages in central Japan. For Ecol Manage 183: 177–193

Nagaike T, Kamitani T, Nakashizuka T (2005) Effects of different forest management systems on plant species diversity in a *Fagus crenata* forested landscape of central Japan. Can J For Res 35: 2832–2841

Nagaike T, Hayashi A, Kubo M, Abe M, Arai N (2006) Plant species diversity in a managed forest landscape composed of *Larix kaempferi* plantations and abandoned coppice forests in central Japan. For Sci 52 (3): 324–332

Numata M, Yoshizawa N eds (2002) Weed flora of Japan. Zenkoku Noson Kyoiku Kyoukai, Tokyo. [In Japanese.]

Ramovs B V, Roberts M R (2003) Understory vegetation and environment responses to tillage, forest harvesting and conifer plantation management. Ecol Appl 13: 1682–1700

Roberts M R, Gilliam F S (1995) Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol Appl 5: 969–977

SAS Institute (2001) JMP user's guide. Version 5.0.1J, SAS Institute, Cary, North Carolina, USA.

Scherer G, Zabowski D, Java B, Everett R (2000) Timber harvesting residue treatment. Part II. Understory vegetation response. For Ecol Manage 126: 35–50

Scherer-Lorenzen M, Körner Ch, E.-D Schulze eds (2005) Forest Diversity and Function: Temperate and Boreal Systems, Springer Verlag, Berlin.

Schoonmaker P, McKee A (1988) Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. For Sci 34: 960–979

Smith T M , Shugart H H & Woodward F I eds (1997) Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge.

Stapanian M A, Sundberg S D, Baumgardner G A, Liston A (1998) Alien plant species composition and associations with anthropogenic disturbance in North American forests. Pl Ecol 139: 49–62

Suzuki W (2002) Forest vegetation in and around Ogawa Forest Reserve in relation to human impact. Ecol Studies 158: 25–41

Tanaka H, Shibata M, Masaki T, Iida S, Niiyama K, Abe S, Kominami Y, Nakashizuka T (2007) Comparative demography of three coexisting maples in gaps and under a closed canopy. J Veg Sci, in press