

Snag Abundance and Species Composition in a Managed Forest Landscape in Central Japan Composed of *Larix kaempferi* Plantations and Secondary Broadleaf Forests

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Nagaike, T. 2009. Snag abundance and species composition in a managed forest landscape in central Japan composed of *Larix kaempferi* plantations and secondary broadleaf forests. *Silva Fennica* 43(5): 755–766.

Larix kaempferi is the main plantation species in the low-snow, cool-temperate zone of Japan. I studied *L. kaempferi* plantations of various stand ages in central Japan to examine and compare the effect of stand age on the abundance, size, and species composition of snags (standing dead trees) compared to those in secondary broadleaf forests. Plantations that were older than the standard rotation age had more and larger snags than young plantations, and the species diversity of snags was positively correlated with stand age. Because the density of living planted *L. kaempferi* showed little correlation with snag variables, whereas that of naturally regenerated tree species was positively correlated with snag variables, the density dependence of snag occurrence was stronger in naturally regenerated trees than in planted *L. kaempferi*. Snag species that were positively correlated with stand age were the main species in secondary broadleaf forests in this area. Basal area, density, and number of species of snags in standard-rotation plantations were significantly lower than in long-rotation plantations and secondary broadleaf forests. Long-rotation plantations are useful for retaining snags compared to standard-rotation plantations.

Keywords long-rotation plantation, plantation age, snags, species composition

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Received 26 May 2008 **Revised** 12 December 2008 **Accepted** 25 August 2009

Available at <http://www.metla.fi/silvafennica/full/sf43/sf435755.pdf>

1 Introduction

Snags (standing dead trees) are an important natural element and are essential for maintaining biodiversity in forest ecosystems (e.g., Ferris and Humphrey 1999, McComb and Lindenmayer 1999, Lindenmayer and Franklin 2002). Because forest managers attempt to minimize decay and mortality of trees to reduce the risk of insect and disease outbreaks and fire and logging hazards (e.g., Egan 1996, Matsuoka and Takada 1999, Garber et al. 2005) and to maximize the space available for superior growing stock (Nyland 1996), snags are considered undesirable in forest management (Hagan and Grove 1999). Thus, few snags are found in managed forests (Sturtevant et al. 1997, Hodge and Peterken 1998, Ganey and Vojta 2005) because intensive stand management usually involves the removal of diseased or dead wood (Fridman and Walheim 2000, Greif and Archibold 2000). However, such features of forest ecosystems cannot be ignored because the maintenance of natural forest components in managed forests is necessary for ecosystem-based forest management (e.g., Moore and Allen 1999, Lindenmayer and Franklin 2002). Therefore, studies of snags have been conducted in managed forests (e.g., Goodburn and Lorimer 1998, Hodge and Peterken 1998, Hale et al. 1999), as well as in primary and old-growth forests (e.g., Stewart and Burrows 1994, Yamanaka et al. 1997, Busing and Fujimori 2005).

Increasingly, snags have been studied in managed forests to determine snag dynamics, longevity, and recruitment (Stephens 2004, Chambers and Mast 2005, Ganey and Vojta 2005), effects of slope aspect, edaphic factors, and topography (Gale 2000, Clark et al. 2002, Økland et al. 2003), changes in abundance with latitude (Gibbs et al. 1993), and nitrogen and carbon storage and decomposition (Yatskov et al. 2003, Creed et al. 2004, Kupferschmid and Bugmann 2005). In addition, snags in managed forests provide important habitat for cavity-nesting birds (Ganey and Vojta 2004, Chambers and Mast 2005, Spiering and Knight 2005), breeding birds (Greenberg and Lanham 2001), and other fauna that use hollows in trees (Gibbons et al. 2002, Lindhe et al. 2005). Moreover, snag abundance is considerably affected by different management regimes (Pedlar

et al. 2002, Ganey and Vojta 2005, Stephens and Moghaddas 2005). For example, Angers et al. (2005) found that snag density was more than twice as high in diameter-limited cuts than in old-growth and 12-year-old selective cuts in northern hardwood stands in Québec, Canada. Carmona et al. (2002) found that snag density and volume were high in early successional areas, but low in old-growth areas in a temperate forest in Chile, whereas Spetich et al. (1999) found that snag volume was greater in old-growth than in second-growth stands in a forest in the midwestern USA. However, studies of snags (Green and Peterken 1997, Moorman et al. 1999, Gjerde et al. 2005) and coarse woody debris (CWD; Kanowski et al. 2003, McCay and Kamoroski 2004) in plantations are limited. Although self-thinning processes of planted trees in plantations have been studied to develop the growth models and predict the yield (e.g., John and James 1977), such studies were focusing on how to minimize snags by management (e.g., thinning) and there were few studies focusing on snags of both planted and naturally regenerated trees in plantations.

Plantation management has changed from having a single objective (e.g., timber production) to having multiple objectives (e.g., habitat for wildlife and plants; Hansen et al. 1991, Moore and Allen 1999). From a landscape perspective, plantations are an important element in intensively managed landscapes where few primary and old-growth forests remain, and may act as substitutes for such forests. In Japan, 40% of forest area is occupied by plantations. Thus, the plantations had been seriously affected local biological diversity. Consequently, some of plantations in Japan are required for ecological restoration to maintain biological diversity and other objectives (Forestry Agency of Japan 2006). The stand age of plantations is one of the most important attributes in forest management because it is closely related to timber size, stand development and corresponding competition among trees. Since species composition changes along a gradient of stand age of plantations (Nagaike et al. 2006), species composition of snags depends on the species occurring in the plots. It is important to determine the species composition of snags because some animals depend on specific species of snags (Lindhe et al. 2005). Long-rotation plantations maintain and

restore species diversity and stand structure much better than standard-rotation plantations (Peterken et al. 1992, Busing and Garman 2002, Nagaike and Hayashi 2004), although empirical data to show an ecological function of long-rotation plantations are still limited. Stem exclusion with stand maturation, one of the main factors regenerating snags, is also closely related to stand age (Oliver and Larsen 1996, Lee et al. 1997). Relationships between snag abundance and stand age in managed forests vary from insignificant and inconsistent (Clark et al. 1998, Grove 2001, DeWalt et al. 2003) to positive (Mannan et al. 1980, Sturtevant et al. 1997, Lee 1998, Hale et al. 1999). However, because these studies were not conducted in plantations, similar studies in plantations are required to develop ecologically sustainable plantation management guidelines. Only Moorman et al. (1999) have previously examined snag abundance in plantations of differing ages.

I studied plantations of various stand ages of *Larix kaempferi*, the main plantation species in the low-snow, cool-temperate zone of central Japan, to examine the effect of stand age on the abundance and size of snags, and to determine the species composition of snags. I also compared snags among standard- and long-rotation plantations and in secondary broadleaf forests, which are an important forest type in landscapes from which primary forests have disappeared.

2 Methods

2.1 Study Site

The study was conducted inutama, Yamanashi Prefecture, in the low-snow, cool-temperate zone of central Japan (1200–1600 m above sea level; 35° N, 138° E). The mean annual precipitation was approximately 1120 mm, and the mean annual temperature was 9.9 °C; snow cover in winter was less than 1 m. The original vegetation of this area is thought to have been mixed forest dominated by *Quercus crispula*, *Fagus japonica*, and *Abies homolepis*. Primary and old-growth forests have been replaced by managed *L. kaempferi* plantations and secondary deciduous broadleaf coppice forests that are now abandoned (hereafter, called

secondary forests), creating a mosaic landscape. I compared snag abundance and species composition between plantation and secondary broadleaf forest to examine the effects of different forest management regimes, because all primary forest in this area has been converted to managed forest. Young secondary forests are rare in this landscape because the gathering of fuelwood and wood to make charcoal was abandoned in the 1960s. Consequently, the current landscape was composed of different-aged *L. kaempferi* plantations and approximately 50-year-old secondary broadleaf forest. Because the standard rotation age of *L. kaempferi* plantations in this region is 50 years, those more than 50 years old were considered long-rotation plantations. In secondary forest, the dominant species were *Quercus crispula*, *Prunus maximowiczii*, and *Betula platyphylla*.

2.2 Field Study

I established one 10 × 100-m study plot in each of 29 *L. kaempferi* plantation stands differing in age (2–77 years old) and in seven deciduous broadleaf secondary forests during 1999–2002 (36 plots in total). To select plantation stands for this study, I applied the following procedure. First, I checked the age distribution of plantations in the study area from the forest register. Second, I selected candidate stands, which carefully selected typical and average plantation stands from the whole age class range of the study area. Third, when the candidate stands were fallen under the categories of extremely different site condition and tending in the past, such stands were excluded. Finally, I randomly selected the study stands from the candidate stands. All plantation plots were single-aged and had experienced the same management procedure (i.e., initial planting density of 2300 trees ha⁻¹, weeding twice before they were 20 years old, thinning twice before they were 40 years old). In plantations ≥ 12 years old, I chose stands that had not been managed for 5 years or more. I used long, narrow plots to include topographical variation in each stand and to minimize the differences in the natural conditions of each forest type (Nagaike et al., 2006). Since the number of years after last management (e.g., thinning) has a significant positive correlation with stand age,

Table 1. Stand age and structure variables (mean DBH, basal area and stem density) of the studied stands.

	Plantation (n=29)			Secondary forest (n=7)		
	Min	Max	Mean	Min	Max	Mean
Stand age	2	77	33.7	≈50	≈50	≈50
Mean DBH (cm)						
Planted <i>Larix kaempferi</i>	3.5	41.3	20.4	-	-	-
Other species	4.0	13.2	7.2	10.9	14.6	12.7
Total	3.5	20.2	12.2	10.9	14.6	12.7
Basal area (m ² /ha)						
Planted <i>Larix kaempferi</i>	0.0	35.7	18.9	-	-	-
Other species	0.0	16.7	4.5	27.7	72.4	38.5
Total	0.0	45.3	23.4	27.7	72.4	38.5
Stem density (/ha)						
Planted <i>Larix kaempferi</i>	0.0	1540.0	637.9	-	-	-
Other species	0.0	2010.0	625.5	1200.0	2210.0	1764.3
Total	0.0	2340.0	1263.4	1200.0	2210.0	1764.3

DBH: Diameter at breast height.

older plantations have experienced a longer time since the last management (Nagaike et al. 2006). In secondary forests in which the stand age of each stand was approximated as 50 years based on analyses of tree ring cores (Nagaike and Hayashi 2004), coppicing had been abandoned in all plots for more than 30 years. In the study area, there were no young secondary forests because of cessation of coppicing.

In each plot, all live trees and snags more than 3 cm in diameter at breast height (DBH) and 2 m in height were identified, and the DBH was measured. Snags that were heavily decayed and difficult to identify to species were broadly classified as conifer or broadleaf trees. The structural variables of plantations and secondary forests are shown in Table 1.

2.3 Analysis

To identify relationships between stand structure variables (e.g., stem density and size) and indices of snag species diversity and stand age for plantations, I calculated Kendall's non-parametric coefficient of correlation (i.e., Kendall's τ) because the data had non-homogeneity and non-normality. Because there was a significant positive correlation

between stand age and time (years) since the last management procedure (e.g., thinning; $\tau=0.766$, $p<0.0001$, Nagaike et al. 2006), I used stand age as the primary factor affecting snag variables. I used a Mann-Whitney U -test to compare stand structure variables and indices of snag species diversity between plantations and secondary forests and a Kruskal-Wallis test with adjusted Bonferroni multiple comparisons to compare among standard (34–43 years) and long-rotation plantations (57–78 years), and secondary forests.

Snag species diversity and richness in each plot were quantified using the Shannon-Wiener diversity index (H' ; Magurran 2004), evenness (J' ; Magurran 2004), and the number of species per unit area. H' and J' were calculated from the stem density of each species per plot using the following formulae:

$$H' = -\sum_{i=1}^m p_i \ln p_i$$

$$J' = H' / \ln m$$

where p_i is the stem density of snags of each species relative to the total density of all species in each plot, and m is the number of species in each plot. In the analysis, snags that could not be identified to species were omitted. To determine

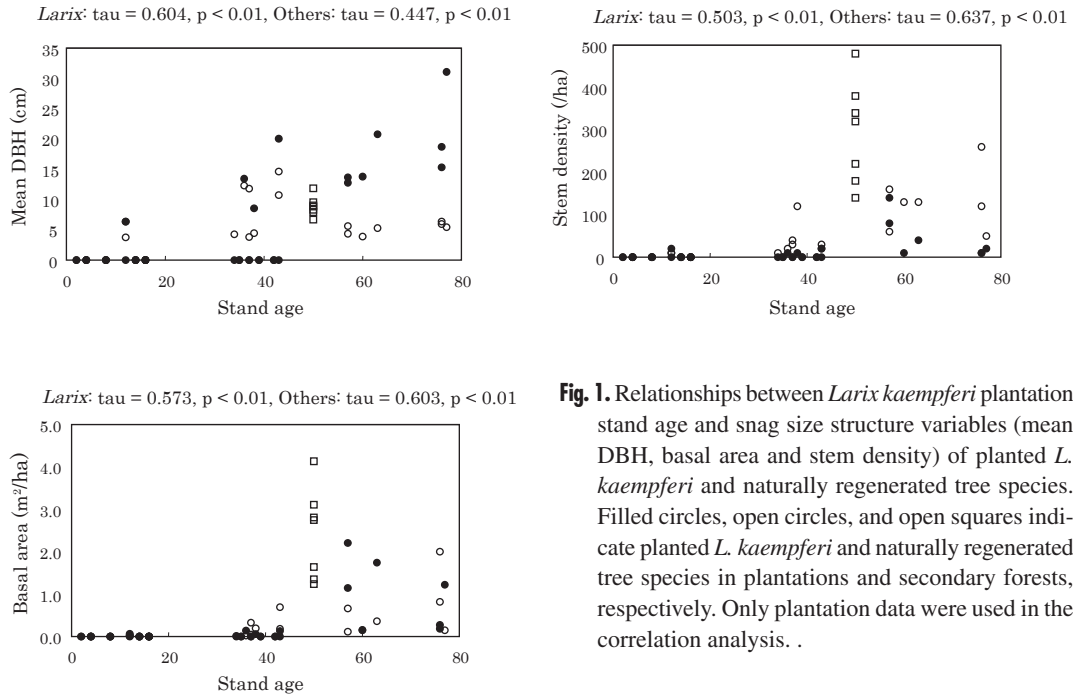


Fig. 1. Relationships between *Larix kaempferi* plantation stand age and snag size structure variables (mean DBH, basal area and stem density) of planted *L. kaempferi* and naturally regenerated tree species. Filled circles, open circles, and open squares indicate planted *L. kaempferi* and naturally regenerated tree species in plantations and secondary forests, respectively. Only plantation data were used in the correlation analysis. .

which species were affected by stand age, I calculated Kendall's τ between snag size structure variables for each species and stand age.

Kendall's τ correlations, the Mann-Whitney *U*-test, and the Kruskal-Wallis test with adjusted Bonferroni multiple comparisons were performed using SPSS version 11.5J (SPSS Inc. 2002).

3 Results

3.1 Changes in Snag Size Structure with Stand Age in Plantations

Because the correlation between the stem density of species other than planted *L. kaempferi* (i.e., naturally regenerated species) and stand age was positive ($\tau = 0.652$, $p < 0.01$), the relative dominance of planted *L. kaempferi* significantly decreased with stand age ($\tau = -0.285$, $p < 0.05$), indicating that older plantations became mixed forests containing naturally regenerated tree species (Nagaike et al. 2006).

The average number of snags in plantations and secondary forests was 71 and 294 stems ha^{-1} , respectively. DBH ($\tau = 0.497$, $p < 0.01$), basal area ($\tau = 0.636$, $p < 0.01$), and density ($\tau = 0.627$, $p < 0.01$) of snags were positively correlated with plantation stand age, indicating that older plantations had more and larger snags than young plantations. Secondary forests had significantly more and larger snags than plantations (DBH, $p < 0.05$; basal area, $p < 0.01$; density, $p < 0.01$).

I also compared the size structure variables (DBH, basal area and density) between planted *L. kaempferi* and the naturally regenerated tree species (Fig. 1). The DBH, basal area, and density of both planted *L. kaempferi* and naturally regenerated trees were significantly positively correlated with stand age. In older plantations, larger snags were mostly comprised of planted *L. kaempferi*. However, in intermediate-aged plantations (about 40 years old), the naturally regenerated trees were more abundant and larger than planted *L. kaempferi* in some study plots. The density of live, planted *L. kaempferi* was negatively correlated with the snag density of naturally regenerated tree

Table 2. Correlation coefficients (Kendall's τ) of size structure variables (basal area and stem density) between live trees and snags in *Larix kaempferi* plantations.

	Basal area of snags			Stem density of snags		
	Planted <i>Larix kaempferi</i>	Naturally regenerated tree species	Total	Planted <i>Larix kaempferi</i>	Naturally regenerated tree species	Total
Basal area of living trees						
Planted <i>Larix kaempferi</i>	0.265	0.285 *	0.329 *	0.295 *	0.341 *	0.358 *
Naturally regenerated tree species	0.510 **	0.704 **	0.649 **	0.495 **	0.659 **	0.655 **
Total	0.434 **	0.499 **	0.521 **	0.442 **	0.512 **	0.531 **
Stem density of living trees						
Planted <i>Larix kaempferi</i>	-0.273	-0.273	-0.262	-0.180	-0.301 *	-0.257
Naturally regenerated tree species	0.592 **	0.666 **	0.672 **	0.540 **	0.732 **	0.734 **
Total	0.389 **	0.375 **	0.375 **	0.403 **	0.390 **	0.436 **

** : $p < 0.01$, * : $p < 0.05$

Table 3. Correlation coefficients (Kendall's τ) between stand age and snag size structure variables (mean DBH, basal area and stem density) in *Larix kaempferi* plantations.

Species name	Mean DBH	Basal area	Stem density
<i>Abies homolepis</i>	0.134	0.134	0.134
<i>Acer mono</i>	0.266	0.266	0.266
<i>Aralia elata</i>	0.095	0.095	0.114
<i>Betula davurica</i>	0.238	0.238	0.238
<i>Betula platyphylla</i>	0.238	0.238	0.238
<i>Castanea crenata</i>	0.162	0.162	0.162
<i>Corylus sieboldiana</i>	0.278	0.292	0.292
<i>Euonymus oxyphyllus</i>	0.162	0.162	0.162
<i>Euonymus sieboldianus</i>	0.375 *	0.384 *	0.381 *
<i>Fraxinus langinosa</i>	0.162	0.162	0.162
<i>Hydrangea paniculata</i>	0.197	0.197	0.197
<i>Kalopanax pictus</i>	0.204	0.204	0.204
<i>Ligustrum tschonoskii</i>	0.326 *	0.326 *	0.326 *
<i>Phellodendron amurense</i>	0.238	0.238	0.238
<i>Prunus grayana</i>	0.149	0.149	0.149
<i>Prunus leveilleana koehne</i>	0.162	0.162	0.162
<i>Prunus maximowiczii</i>	0.485 **	0.503 **	0.494 **
<i>Quercus crispula</i>	0.386 *	0.386 *	0.386 *
<i>Quercus serrata</i>	0.162	0.162	0.162
<i>Rhus trichocarpa</i>	0.238	0.238	0.238
<i>Salix bakko</i>	-0.162	-0.162	-0.162
<i>Sambucus racemosa</i>	0.128	0.146	0.152
<i>Sorbus alnifolia</i>	0.162	0.162	0.162
<i>Weigela decora</i>	0.238	0.238	0.238
Planted <i>Larix kaempferi</i>	0.634 **	0.566 **	0.493 **

DBH: Diameter at breast height, **: $p < 0.01$, * : $p < 0.05$.

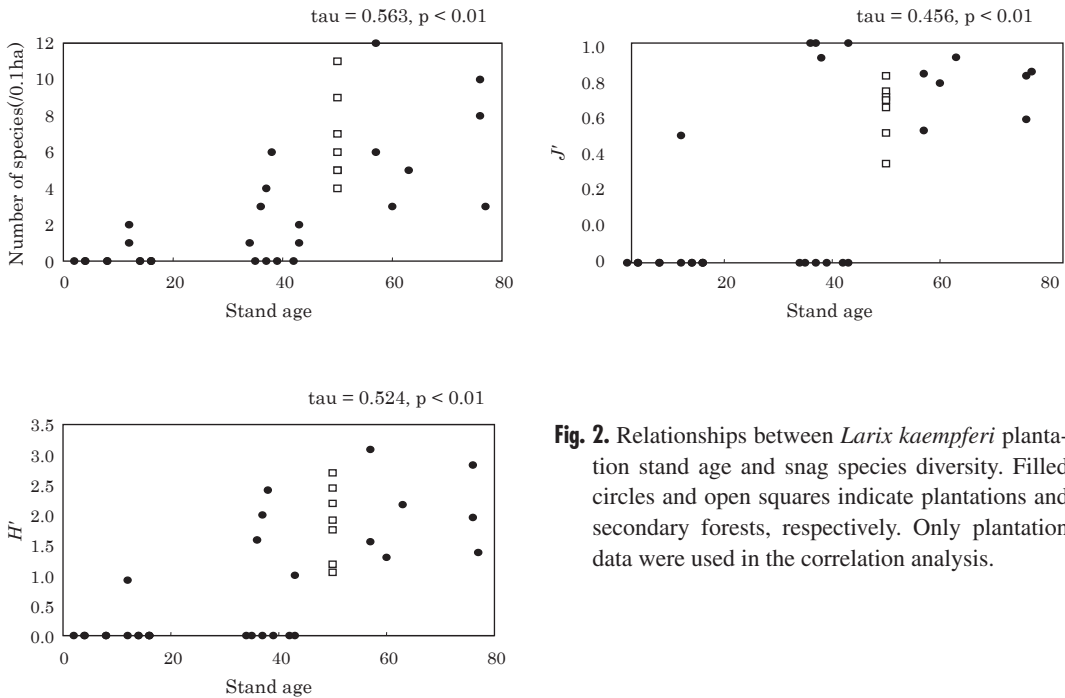


Fig. 2. Relationships between *Larix kaempferi* plantation stand age and snag species diversity. Filled circles and open squares indicate plantations and secondary forests, respectively. Only plantation data were used in the correlation analysis.

species, but there was no correlation between the density of planted *L. kaempferi* and the basal area of snags (Table 2). However, the basal area of live trees of both planted *L. kaempferi* and naturally regenerated tree species was positively correlated with snag density and basal area (Table 2).

3.2 Species Diversity and Composition of Snags

I found significant positive correlations between the species diversity indices (number of species, H' , and J') of snags and stand age in the plantations (Fig. 2). The number of species and H' were lower in plantations than in secondary forests (number of species, $p < 0.01$; H' , $p < 0.01$), whereas there was no difference in J' ($p = 0.152$). The snag size structure variables of five species (*Euonymus sieboldianus*, *Ligustrum tschonoskii*, *Prunus maximowiczii*, *Quercus crispula*, and planted *L. kaempferi*) among the 36 identified species were positively correlated with stand age (Table 3).

3.3 Comparisons of Snags among Standard- and Long-Rotation Plantations and Secondary Forests

Basal area, stem density, and number of species of snags in standard-rotation plantations were significantly smaller than in long-rotation plantations and secondary forests (Table 4). Moreover, there were no significant differences for those variables between long-rotation plantations and secondary forests.

4 Discussion

Characteristics of dead wood are affected by old and recent historical factors, as well as current processes, such as fire, competitive exclusion, storms, insect outbreaks, and forest management (Hély et al. 2000, Bobiec 2002, Norden et al. 2004). These factors change with stand development, which is closely related to stand age (Oliver

Table 4. Comparisons of structural variables (mean DBH, basal area and stem density) and species diversity indices (Number of species per unit area, H' and J') of snags among standard (34–43 years) and long-rotation plantations (57–78 years) and secondary forests using the Kruskal-Wallis test. When a significant difference was calculated by the test, each pair of forest types was analyzed using a Mann-Whitney U test with adjusted Bonferroni multiple comparisons. Different letters indicate significant differences by adjusted Bonferroni multiple comparisons among forest types at $p < 0.017$.

	Standard-rotation plantations (n=10)		Long-rotation plantations (n=7)		Secondary forests (n=7)		Kruskal-Wallis test (p value)
	Mean	SD	Mean	SD	Mean	SD	
Structural variables							
Mean DBH (cm)	5.6	5.2	8.3	2.6	8.9	1.6	0.246
Basal area (m ² /ha)	0.2	0.2 a	1.6	0.7 b	2.4	1.1 b	0.000
Stem density (/ha)	36.0	41.4 a	237.1	156.7 b	294.3	120.4 b	0.000
Species diversity indices							
Number of species(/0.1ha)	1.7	2.1 a	6.7	3.5 b	6.7	2.5 b	0.002
H'	0.7	1.0	2.0	0.7	1.9	0.6	0.021
J'	0.4	0.5	0.8	0.1	0.7	0.1	0.382

SD: Standard deviation, DBH: Diameter at breast height, H' : Shannon's diversity index, J' : Equitability.

and Larsen 1996). I found a significant positive correlation between snag size and abundance and stand age in plantations. Some studies have shown a similar relationship in non-plantation managed forests (Sturtevant et al. 1997, Lee 1998, Hale et al. 1999). Jenkins et al. (2004) found that mature stands had a relatively low basal area of standing dead wood compared to older silvicultural openings, which were still undergoing stem exclusion in hardwood forests. Similarly, Moorman et al. (1999), who examined snags in plantations, found that snag density was lowest in the oldest loblolly pine plantations in South Carolina, USA, and suggested that regenerating stands may have high densities of small snags as a result of density-dependent tree mortality. Snags are mostly created by self-thinning during the stem-exclusion phase of stand development (Bobiec 2002, Norden et al. 2004, Angers et al. 2005). Young *L. kaempferi* plantations had undergone recent management (e.g., weeding), whereas older plantations had not (Nagaike et al. 2006). As a result, naturally regenerated tree species were abundant in older plantations, and self-thinning appeared to occur within these plantations. Therefore, the differences between *L. kaempferi* and loblolly pine plantations may have been dependent on the timing of management (i.e., thinning).

In addition, older *L. kaempferi* are more prone to infestations of heart-rot disease than are younger individuals (Ohsawa et al. 1994). Thus, these reasons may explain why my results differ from those of Moorman et al. (1999).

Snag abundance was considerably lower in *L. kaempferi* plantations than in secondary forest, similar to the results of McComb et al. (1986), Green and Peterken (1997), and Moorman et al. (1999), indicating that plantations have fewer snags than other forest types. The secondary forest appeared to undergo severe self-thinning, whereas this process was weak in plantations because of previous management procedures, which included the removal of snags and control of stock density (i.e., thinning). However, long-rotation plantations have almost the same abundance of snags as secondary forests (Table 4). This result suggested that long-rotation plantations could mitigate the effects of removal of snags from young plantations.

The species composition of snags differed with stand age (Fig. 1). In older plantations, *L. kaempferi* snags were larger than those of naturally regenerated tree species. In contrast, there were more snags of naturally regenerated tree species in some 40-year-old plantations than in older plantations, because naturally regenerated tree

species seemed to suffer from self-thinning and suppression by planted *L. kaempferi* in some 40-year-old plantations. Lee (1998) reported that the self-thinning of small trees was supplemented by the death of canopy co-dominants. Webster and Jenkins (2005) showed that snag density was positively correlated with live tree density, and snag basal area was also positively correlated with the mean DBH of live trees. I found little correlation between the density of live planted *L. kaempferi* and snag variables, but a significant positive correlation between naturally regenerated tree species and snag variables (Table 2), suggesting that the density-dependence of snag occurrence was stronger in naturally regenerated trees than in planted *L. kaempferi*. Because the density of planted *L. kaempferi* ≥ 20 years old was controlled by thinning, self-thinning would have rarely occurred among the planted trees, unless older plantations were infected by heart-rot disease. Also, because older *L. kaempferi* plantations had more naturally regenerated tree species (Nagaike et al. 2006), the snag density of naturally regenerated trees was higher in older plantations.

Snag species diversity (number of species and H') was positively correlated with stand age, and in four species (not including planted *L. kaempferi*) snag abundance was positively correlated with stand age. Angers et al. (2005) found that high snag density was created by self-thinning of the post-harvest cohort caused by the death of short-lived species in limited-diameter cuts. Snag species composition differs with anthropogenic disturbance history (Webster and Jenkins 2005), and the occurrence of a variety of snag species attracts many species of animals because of different faunal preferences for various snag species (Lindenmayer et al. 2000, Mazurek and Zielinski 2004). Hale et al. (1999) showed that older extended-rotations in managed hardwood forests in Minnesota, USA, may have similar snag species compositions to old-growth forests. Snag species that were positively correlated with stand age (Table 3) were the main species in secondary forests in my study area (Nagaike et al. unpublished data). Consequently, the results were similar to the present study in a plantation.

The ecological characteristics and functions of long-rotation plantations, such as stand structure, species composition of the understory, and

biomass accumulation, have been evaluated (e.g., Peterken et al. 1992, Busing and Garman 2002, Nagaike et al. 2003). I showed that long-rotation plantations have more and larger snags than young plantations (Table 4), and that snag species diversity was positively correlated with stand age. Many authors agree that large living and dead trees have greater biological value than small ones (Harmon et al. 1986, Ganey 1999, Angers et al. 2005). Because a snag is future downed wood, which is an important element of forest ecosystems (Lee et al. 1997, Webster and Jenkins 2005), the retention of large trees as future snags is necessary in managed forests (Ganey 1999, Moore and Allen 1999, Spiering and Knight 2005). Moorman et al. (1999) also recommended the retention of designated old, large-diameter trees that can be converted to snags to promote suitable habitat for cavity-nesting species, especially in young pine plantations. Therefore, long-rotation plantations are useful in retaining large snags for ecologically sustainable plantation management.

Acknowledgments

I thank Atsuko Hayashi, Masako Kubo, Midori Abe, and Nobumasa Arai for help with data collection in the field. I also thank the staff of the Yamanashi Forest Research Institute, the Prefectural Forest Division, and the Kyohoku Forest Office of Yamanashi Prefecture for kind encouragement. This research was part of the "Forest Ecosystem Monitoring Project" of Yamanashi Prefecture, the research project "Sustainability and Biodiversity Assessment of Forest Utilization Options" of the Research Institute for Humanity and Nature, Japan, and "Development of Regeneration Technology for Leading Artificial Coniferous Forests to Broadleaf Forests" of the Research and development projects for application in promoting new policy of Agriculture, Forestry and Fisheries.

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