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ORIGINAL ARTICLE

Effects of previous forest types and site conditions on species composition and abundance of naturally regenerated trees in young *Cryptomeria japonica* plantations in northern Japan

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Abstract Naturally regenerated trees in young *Cryptomeria japonica* plantations were investigated in 141 quadrats of 10 × 50 m within a watershed of 1,000 ha, and factors affecting their composition and abundance were examined. The species composition of naturally regenerated trees was classified into four types. Dominant species were *Swida controversa*, *Magnolia hypoleuca* and *Pterocarya rhoifolia* in Type A1, *Betula maximowicziana, M. hypoleuca*, *Quercus crispula* and *Castanea crenata* in Type A2, *Q. serrata* and *C. crenata* in Type B1, and *Pinus densiflora* in Type B2. The results of path analysis showed significant influences of previous forest type and geology among the factors that correlated with the species composition of naturally regenerated trees; previous forest type in particular showed a higher absolute path coefficient value. Species composition types of naturally regenerated trees corresponded to the previous forest types: Types (A1 and A2) corresponded to the natural forests composed of *Thujopsis dolabrata* var. *hondai*, *Fagus crenata*, *Aesculus turbinata*, etc., Type B1 corresponded to the secondary *Q. crispula* and *Q. serrata* forest, and Type B2 corresponded to the secondary *P. densiflora* forest, respectively. The abundance of naturally regenerated trees was strongly affected by geology; i.e., plantations on soft-sedimentary dacitic tuff contained great amounts of colonizing *P. densiflora* trees.

Keywords Conifer plantations · Naturally regenerated trees · Previous forest type · Site conditions · Species composition

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Introduction

In conifer plantations, planted conifers are generally accompanied by naturally regenerated trees, through the natural regeneration originating from trees that existed before the establishment of the plantations, or colonization from surrounding natural forests (e.g., Hérault et al. 2005; Kint et al. 2006). Recently, the value of such naturally regenerated trees in conifer plantations has been recognized, because those trees are expected to play important roles in environmental conservation and in the maintenance of biological diversity, as well as in the promotion of hardwood resources (Cannell et al. 1992; Moore and Allen 1999; Cameron et al. 2001).

In Japan, conifer plantations occupy ca. 40% of the total forest area resulting from the afforestation that was promoted mainly in the 1960s; however, conifers often grow much less abundantly than expected in some cases, especially in high-altitude areas or heavy snowfall regions (Yokoi and Yamaguchi 2000a; Masaki et al. 2004). In many cases, such unsuccessful plantations contain many native hardwood trees and are becoming conifer–hardwood mixed forests (Yokoi and Yamaguchi 1998). It would be wise to manage those plantations as mixed forests with naturally regenerated hardwoods to enhance their multiple functions (Yokoi and Yamaguchi 2000b; Masaki et al.

2004). On the other hand, single-species plantations without naturally regenerated trees cause other kinds of serious problems when they cover vast areas; these problems include a decrease in plant species diversity (Kiyono 1990; Nagaike 2000, 2002; Ito et al. 2003) and the deterioration of the forest as a wildlife habitat. Colonization of various hardwoods into plantations is expected to solve such problems (Fujimori 2001). Thus, management methods that make the best use of naturally regenerated trees have attracted a great deal of attention as a new approach to plantation practice.

Various factors are related to the occurrence of naturally regenerated trees in plantations, e.g., previous vegetation types, site conditions, snow conditions (Yokoi and Yamaguchi 2000a), species planted, stand age (Oberhauser 1997), and distance from seed sources (Parrotta 1995; Kodani 2006; Utsugi et al. 2006). Among these factors, the previous vegetation present before the establishment of a plantation and the land-use pattern that controlled the previous vegetation type strongly affect the species diversity and composition of naturally regenerated trees in the plantations. The vegetation of a plantation differs greatly according to whether the previous vegetation was forest, pasture, meadow or agricultural land (e.g., Hill and Jones 1978; Sykes et al. 1989; Wallace and Good 1995; Koerner et al. 1997; Ito et al. 2004; Wulf 2004). The occurrence of naturally regenerated trees in plantations may differ according to the previous forest type; e.g., a primeval forest showing little influence of human impact or a secondary forest regenerating after human disturbance. However, the influence of previous forest type has not been examined. Some studies have highlighted the influences of site conditions in terms of geological and topographic factors on the occurrence of naturally regenerated trees; e.g., slope positions (Maeda 1992), slope aspect (Masaki et al. 2004), inclination and profile of slope (Yokoi and Yamaguchi 2000a), and soil fertility (Ferris et al. 2000). The influences of these site conditions should be clarified in detail. In addition, few studies have clarified the relationships among factors that affect naturally regenerated trees in plantations, and which factor is the most critical. Such examinations would contribute to a better understanding of the occurrence of naturally regenerated trees, and to the establishment of guidelines for new plantation practices.

In the present study, factors that affect the species composition and abundance of naturally regenerated trees and the causal relations among such factors were examined in young, 11 to 30 year-old *Cryptomeria japonica* plantations in a watershed of ca. 1,000 ha in northern Japan. The study focused on the influences of the previous forest type and site conditions in terms of geological and topographic factors.

Materials and methods

Study region

The study region is the Omyojin Experimental Forest of Iwate University in Shizukuishi Town, Iwate Prefecture, northern Tohoku District, Japan (39°40′N, 140°54′E). The region generally corresponds to the watershed of the Akasawa River (ca. 1,000 ha), from the hilly area in its lower reaches to the mountainous area in its upper reaches, with an altitude of 230–682 m. Geological and topographic features are described as follows (Tada 1976):

1. The hilly area is gentle and contains flood plains with thin gravel beds including terraces. It consists of dacitic tuff classified as Miocene Series of Neogene–Tertiary System, which are relatively soft sediments that are easily eroded.
2. The mountainous area consists of sedimentary rock such as tuff, shale, and, in parts, volcanic rocks such as rhyolite, dacite, also classified as Miocene Series of Neogene–Tertiary System, but these rocks are older than the rocks in the hilly area. The slopes are usually steep, with an inclination of 25–35°, but the relief is relatively small.

The meteorological observation data (1977–1986) at the office of the Omyojin Experimental Forest located at the lowest reaches of the region (altitude 240 m) indicate 75.1 in WI, −27.0 in CI, 1,655 mm in annual precipitation, and 85 cm in maximum snow depth. According to the maximum snow depth map by Kojima (1975), maximum snow depth in the mountainous area in and around the study region is about 150 cm, indicating relatively mild snow conditions within the mountainous regions of the northern Tohoku District.

Natural forests of the Omyojin Experimental Forest are roughly divided into three types as follows (Sugita 1990).

1. *Pinus*-type: the hilly area is covered with *Pinus densiflora* forest. This area had been used as meadows and pastures until the establishment of the Omyojin Experimental Forest in 1905. After its utilization as grassland was stopped, *P. densiflora* secondary forest was formed.
2. *Quercus*-type: the lower reaches of the mountainous area located relatively near villages are covered with deciduous hardwood forest dominated by *Quercus serrata* and *Q. crispula*, accompanied by *P. densiflora*, *Castanea crenata*, *Magnolia hypoleuca* and *Prunus verecunda*. This type is secondary forest, because felling for firewood had long been performed here.
3. *Thujopsis*, *Fagus*, *Aesculus*-type: the upper reaches of the mountainous area are covered with mixed forests

consisting of *Thujopsis dolabrata* var. *hondai*, *Fagus crenata*, *Aesculus turbinata*, *C. japonica*, *Q. crispula*, *Acer mayrii*, *M. hypoleuca*, and *Pterocarya rhoifolia*. *Thujopsis dolabrata* var. *hondai* is dominant on ridges and *A. turbinata* in valleys. Forest consisting of these tree species has remained in an almost primeval state because of the relatively low impact of humans in this area.

Conifer plantations cover 28% of the area of the Omyojin Experimental Forest, in which *C. japonica* plantations occupy 65%. In terms of the age distribution of conifer plantations, stands planted in 1961–1970, when the so-called expansive afforestation project was actively executed, occupied 54% of the area of *C. japonica* plantations. Previous forests of those plantations were natural forests and secondary forests, no stands were created after cutting previous plantations. As a rule, weeding should have been performed for six years after planting. Cleaning should have been performed until the stands were 13 years old; however, it may not have been executed in some cases. The composition and structure of the conifer plantations was outlined in Sugita et al. (2007).

Data

The data from a forest survey of the Omyojin Experimental Forest carried out in 1983–1985 were used for the analyses. The stands studied were *C. japonica* plantations which were 11–30 years old at that time (planted in 1953–1972). In the forest survey, 141 strip quadrats of size 10 × 50 m were set with their longer sides in the contour direction, at intervals of ca. 20 m in altitude along a slope from valley to ridge. Trees higher than 2 m (shrub species were excluded) in the quadrats were identified and their diameters were measured at breast height (DBH). The DBHs were measured by caliper or ocular estimation and rounded to within 2 cm. Because discrimination between *Prunus sargentii* and *P. verecunda*, among *Acer japonicum, A. sieboldianum* and *A. matsumurae*, between *Fraxinus lanuginosa* and *F. sieboldiana*, and between *Tilia japonica* and *T. maximowicziana* was imperfect, species from each species group were gathered. Native trees that were regarded as being component trees of the previous forest that therefore escaped the felling were excluded from the analyses.

The following parameters were examined for each quadrat as site condition data:

1. Altitude: interpreted from maps and rounded to within 5 m (235–590 m).
2. Stream no.: ordinal number of the watershed of the tributary of the Akasawa River in which a quadrat was located, counted from the lower reaches (1–14).
3. Geology: interpreted from the geological map of the Omyojin Experimental Forest (Tada 1976), classified into two categories: the relatively soft-sedimentary dacitic tuff of the hilly area (code = 1) and not soft-sedimentary rocks of the mountainous area (code = 2).
4. Slope position: classified into four categories: flood plain (code = 1), lower part of a slope (code = 2), middle part of a slope (code = 3), and upper part of a slope (code = 4).
5. Slope aspect: classified into two categories: the flat, N and E (code = 1), and S and W (code = 2); the former may be shady and relatively wet, while the latter may be sunny and relatively dry.

The following parameters were examined for each quadrat as stand condition data:

1. Stand age: the value at the survey time (11–27 years old)
2. Previous forest type: the type of forest which existed before the establishment of a plantation was determined based on past aerial photographs and the surrounding natural forest, and was classified into three categories: the *Pinus* type, the *Quercus* type, and the *Thujopsis*, *Fagus*, *Aesculus* type.

Analysis

Classification and ordination of quadrats by species composition of naturally regenerated trees

Classification in terms of tree species composition of 115 quadrats in which the total relative basal areas of naturally regenerated trees were 1% or more was performed by two-way indicator species analysis (TWINSPAN, Hill 1979b), and the ordination was performed by detrended correspondence analysis (DCA, Hill 1979a). The relative basal area of each tree species compared to the total basal area of naturally regenerated trees was used as a quantitative index of each tree species. The dominant species within naturally regenerated trees were determined by dominance analysis according to the method of Ohsawa (1984).

Analysis of the correlations among factors

The relations between abundance ($n = 141$) or species composition ($n = 115$) of the naturally regenerated trees and each parameter were analyzed, as were the relations among parameters. The correlations were examined using Spearman's rank correlation coefficient.

Parameters with three categories, i.e., previous forest type, were reorganized such that they contained two categories, and this parameter was treated as a rank variable. Because the *Pinus* type is similar to the *Quercus* type in terms of species composition (Sugita 1990), these two types were integrated (code = 1), and the other category comprised the *Thujopsis*, *Fagus*, *Aesculus* type (code = 2).

Analysis of causal relations among factors

Path analysis with structural equation modeling (SEM) was performed in order to examine the causal relations among abundance or the tree species composition of naturally regenerated trees and various parameters. SEM is one of the more comprehensive approaches that enables researchers to analyze interrelationships among variables in multidimensional data, including path model analysis (Pugesek et al. 2003). Several studies on natural forests have attempted to relate understory tree species richness and abundance to stand structural attributes and environmental factors using SEM (Kubota et al. 2004; Laughlin et al. 2007). The categories of previous forest type were also reorganized into two categories in order to be able to treat it as a rank variable. Parameters such as previous forest type, geology and slope aspect were used as exogenous variables in model construction, because they cannot be used as endogenous variables. The models for which the null hypothesis ("the constructed model is adequate") was not rejected ($P > 0.05$) were selected by examining the Bollen–Stine bootstrap probability. The path coefficients and the standard errors were estimated by means of the bootstrapping procedure (2,000 trials), for which multivariate normality was not required because many parameters did not fit to normality. The significance of each standardized path coefficient, representing the strength of the direct effect of one variable on another, was tested with the bias-corrected percentile method (Manly 1997). The analysis was performed using Amos 5.0 (SmallWaters Co., Chicago, IL, USA) computer software.

Table 1 Presence of tree species for the community types (%)

	Community type			
	A1 n=24	A2 52	B1 10	B2 29
Magnolia hypoleuca	83	81	10	14
Swida controversa	96	52		
Prunus grayana	25	37	10	
Pterocarya rhoifolia	46			
Morus bombycis	25	2		
Quercus crispula	21	83	10	28
Styrax obassia	17	37		3
Thujopsis dolabrata var. *hondai*	10	31		
Ilex macropoda	4	27		10
Castanea crenata	29	50	100	90
Acer spp.*		13	40	21
Betula maximowicziana	21	81	30	7
Salix bakko	17	52	60	17
Quercus serrata		12	100	93
Rhus trichocarpa		8	20	17
Robinia pseudoacacia			20	10
Pinus densiflora		4	10	100
Styrax japonica				17
Populus sieboldii				14
Acer mayrii	4	15	10	7
Acanthopanax sciadophylloides	4	12	10	7
Acer rufinerve		12	10	10
Fraxinus spp.**		17		3
Prunus spp.***	4	17		3
Tilia spp. ****	4	15		
Carpinus luxiflora	4	10		3
Prunus ssiori	4	6		7
Phellodendron amurense	17	2		
Alnus hirsuta	4	6		
Kalopanax pictus	4	4		
Carpinus cordata	4	4		
Aesculus turbinata	4			
Aralia elata	4			
Clerodendron trichotomum	4			
Rhus javanica	4	2		
Thuja standishii		2	10	
Acer micranthum		4		
Fagus crenata		2		
Sorbus commixta		2		
Paulownia tomentosa		2		
Hamamelis japonica		10		7
Sorbus alnifolia		4		3
Clethra barbinervis				7

* *Acer japonicum*, *A. sieboldianum*, *A. matsumurae*

** *Fraxinus lanuginosa*, *F. sieboldiana*

*** *Prunus sargentii*, *P. verecunda*

**** *Tilia japonica*, *T. maximowicziana*

Results

Classification and ordination of quadrats by species composition of naturally regenerated trees

One hundred fifteen quadrats were classified into four community types by TWINSPAN (Table 1). First, they were divided roughly into an A group in which *M. hypoleuca* and *S. controversa* frequently occurred and a B group in which *Q. serrata* frequently occurred. The former group was divided into two types: type A1 with *P. rhoifolia* and *Morus bombycis* and type A2 with *Q. crispula*, *Betula maximowicziana*, *Salix bakko*, *C. crenata* and *Styrax obassia*. The latter group was divided into two types: type B1 in which *P. densiflora* scarcely occurred and type B2 in which *P. densiflora* always occurred. The dominant species in each type were *S. controversa, M. hypoleuca* and *P. rhoifolia* in Type A1, *B. maximowicziana*, *Q. crispula, C. crenata* and *M. hypoleuca* in Type A2, *Q. serrata* and *C. crenata* in Type B1, and *P. densiflora* in Type B2 (Table 2). Those dominant species contained species with

Table 2 Average relative basal areas (%) of principal species compared to the total area of naturally regenerated trees for various community types

	Community type				Dispersal agent[b]	Soil seed bank
	A1 $n = 24$	A2 $n = 52$	B1 $n = 10$	B2 $n = 29$		
Pterocarya rhoifolia	12.5[a]				Wind	
Swida controversa	40.7[a]	3.3			Frugivorous vertebrate	Have[c]
Magnolia hypoleuca	23.7[a]	11.2[a]	0.2	0.0	Frugivorous vertebrate	Have[c]
Betula maximowicziana	3.8	35.7[a]	5.1	0.0	Wind	Have[d]
Quercus crispula	1.3	11.0[a]	0.2	0.5	Gravity, rodents	
Castanea crenata	2.6	12.8[a]	36.7[a]	2.9	Gravity, rodents	
Quercus serrata		0.7	36.3[a]	3.8	Gravity, rodents	
Pinus densiflora		0.2	5.8	90.4[a]	Wind	

[a] Dominant species were determined by the dominant analysis according to the method of Ohsawa (1984)

[b] After Hasegawa and Taira (2000), Masaki et al. (2004), etc.

[c] Masaki et al. (2004)

[d] Osumi and Sakurai (1997)

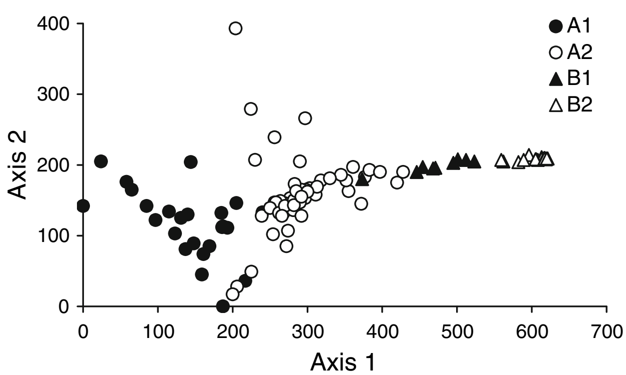

Fig. 1 Ordination of quadrats by detrended correspondence analysis (DCA)

seeds dispersed by wind or frugivorous vertebrate, or with soil seed banks.

Using DCA, quadrats belonging to A1, A2, B1, and B2 were arranged in this order along Axis 1 (see Fig. 1).

Relationships between species composition and parameters for naturally regenerated trees

The DCA Axis 1 score was adopted as a quantitative index of the species composition of naturally regenerated trees because of the high eigenvalue (0.919). The Spearman's rank correlation coefficients obtained between parameters ($n = 115$) are shown in Table 3. Among the seven parameters, six gave significant correlations for all combinations, with the exception being slope aspect. In addition, the correlations between slope aspect and previous forest type and between slope aspect and geology were significant. The parameters which significantly correlated with the DCA Axis 1 score were stand age, slope position, stream no., altitude, geology, and previous forest type. Among these, previous forest type showed the greatest absolute value of the rank correlation coefficient (Table 3).

Using path analysis, 36 ecologically assumable models in which the degree of freedom was not 0 were examined, and only one model was accepted as potentially explaining the DCA score. The path diagram of the model is shown in Fig. 2. Previous forest type and geology showed significant relations to the DCA score, and the absolute value of the path coefficient of previous forest type was higher than that of geology.

Relative frequencies of the community types for previous forest type are shown in relation to the slope position in Fig. 3. For the *Thujopsis*, *Fagus*, *Aesculus* type, Type A2 occupied more than 70% irrespective of slope position, and Type A1 was found to be limited to the middle and lower parts of the slopes. For the *Quercus* type, Type B1 was dominant. For the *Pinus* type, Type B2 occupied more than 70%, and Type B1 was also found.

Relationships between abundance and parameters for naturally regenerated trees

The relation between the DCA Axis 1 score and the relative basal area for naturally regenerated trees is shown in Fig. 4. The relative basal area tended to increase with the DCA score ($r = 0.574$, $P < 0.0001$). Quadrats belonging to Type B2 yielded particularly high values (>40%). However, the correlation was not significant when the quadrats belonging to B2 were excluded ($r = -0.157$, $P = 0.149$).

Spearman's rank correlation coefficients among parameters and between the relative basal area of naturally

Table 3 Spearman's rank correlation coefficients between parameters and the DCA Axis 1 score ($n = 115$)

	Slope aspect	Stand age	Slope position	Stream no.	Altitude	Geology	Previous forest type
Stand age	−0.153 ns						
Slope position	0.117 ns	−0.333***					
Stream No.	0.142 ns	−0.217*	0.198*				
Altitude	0.135 ns	−0.271**	0.392***	0.837***			
Geology	0.304**	−0.588***	0.327***	0.785***	0.792***		
Previous forest type	0.318***	−0.537***	0.373***	0.812***	0.826***	0.907***	
Score of DCA Axis 1	−0.117 ns	0.415***	−0.313***	−0.743***	−0.766***	−0.783***	−0.818***

ns: $P \geq 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

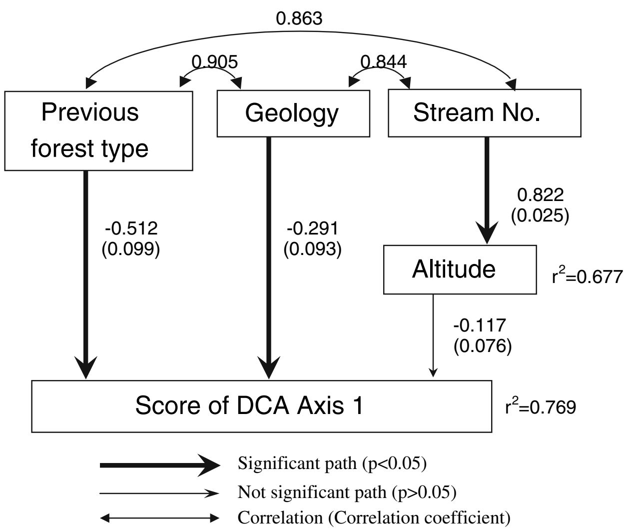

Fig. 2 Path diagram explaining the DCA score; the path coefficient (standard error) is shown. Bollen–Stine bootstrap probability $P = 0.090$

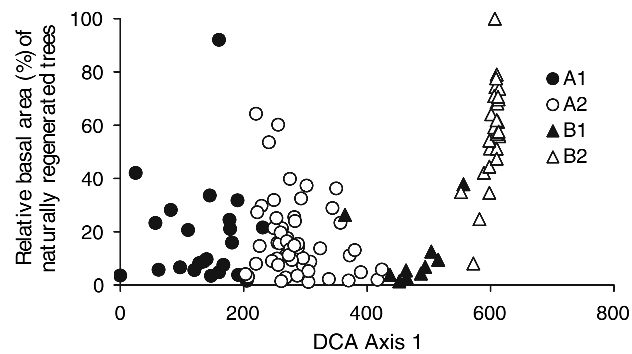

Fig. 4 Relationship between the DCA Axis 1 score and the relative basal area of naturally regenerated trees (for stands with a relative basel area of >1% of naturally regenerated trees, $n = 115$)

regenerated trees and the parameters ($n = 141$) are shown in Table 4. The correlations among parameters were similar to those in Table 3 regardless of the difference in sample size. The parameters which significantly correlated with the relative basal area of naturally regenerated trees were slope position, stream no., altitude, geology, and previous forest type. Among these, geology showed the greatest absolute value of the rank correlation coefficient (Table 4).

Using path analysis, 36 ecologically assumable models in which the degree of freedom was not 0 were examined, and all were rejected as models that explained the relative basal area of naturally regenerated trees.

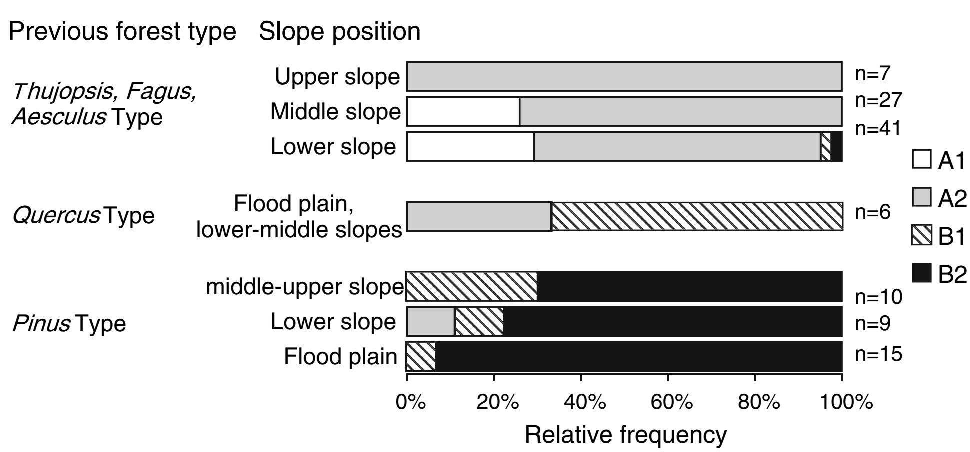

Fig. 3 Relative frequencies of community types for categorical combinations of previous forest types and slope positions

Table 4 Spearman's rank correlation coefficients between parameters and the relative basal area of naturally regenerated trees ($n = 141$)

	Slope aspect	Stand age	Slope position	Stream no.	Altitude	Geology	Previous forest type
Stand age	−0.103 ns						
Slope position	0.042 ns	−0.307***					
Stream no.	0.175*	−0.234**	0.197*				
Altitude	0.101 ns	−0.201*	0.382***	0.802***			
Geology	0.213*	−0.530***	0.322***	0.755***	0.755***		
Previous forest type	0.195*	−0.492***	0.384***	0.775***	0.799***	0.902***	
Relative basal area	0.028 ns	0.148 ns	−0.232**	−0.231**	−0.383***	−0.501***	−0.451***

ns: $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$; *** $P < 0.001$

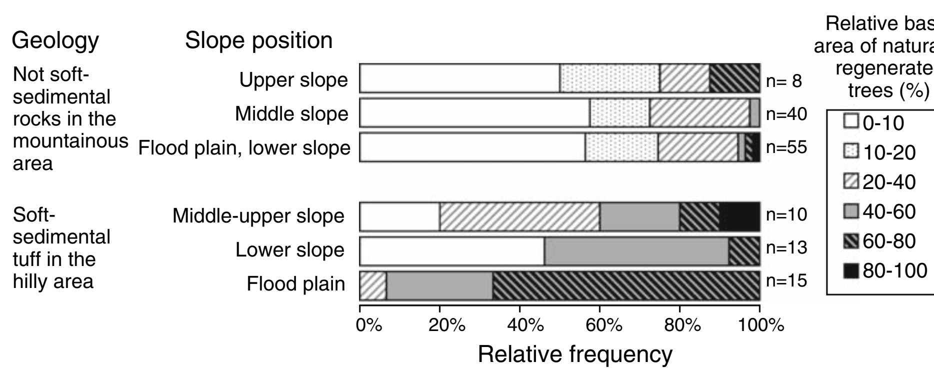

Fig. 5 Relative frequencies of the classes for the relative basal area of naturally regenerated trees in relation to geology and slope position

The relative frequencies of the classes for the relative basal area of naturally regenerated trees for geological categories are shown in Fig. 5. On the relatively soft-sedimentary dacitic tuff in the hilly area, the relative dominance of naturally regenerated trees was high: classes of more than 40% in relative basal area occupied 40–94%, while those classes occupied only 3–13% on rocks that were not soft sediment in the mountainous area.

The variations in the relative dominance of naturally regenerated trees in terms of slope position were not significant, except that naturally regenerated trees were more dominant on the flood plains than on the lower or middle parts of slopes on soft-sediment dacitic tuff in the hilly area (Fig. 5).

Discussion

Factors affecting the composition of naturally regenerated trees

Different types of species composition of naturally regenerated trees in *C. japonica* plantations were recognized within a watershed of 1,000 ha (Table 1), and were arranged along DCA Axis 1 (Fig. 1). The dominant species of naturally regenerated trees contained species with seeds dispersed over long distances by wind or birds, or with soil seed banks that were advantageous for regeneration after disturbances (Table 2), similar to findings reported by previous studies (Hasegawa and Taira 2000; Masaki et al. 2004).

All examined parameters except for slope aspect showed significant correlations with the DCA Axis 1 score, which represented the gradient of species composition of naturally regenerated trees (Table 3). However, these parameters were not independent; instead they showed significant correlation among all combinations. In particular, high correlations were seen among stream no., altitude, geology, and previous forest type (Table 3). Naturally, the altitude rises along the gradient from the lower reaches to the upper reaches of a watershed. Owing to the tectonics in this region, relatively soft-sedimentary dacitic tuff is distributed in the hilly areas of the lower reaches, while comparatively hard rocks are distributed in the mountainous areas of the upper reaches (Tada 1976). Flood plains are widely found in the hilly areas of the lower reaches, while they are rarely found in the mountainous areas of the upper reaches. The lower–upper reaches gradient also reflects the gradient of previous human impact: the intensity and frequency of disturbances due to human activities such as felling, burning, and grazing decreases with distance from the villages; this tendency must produce different types of previous forest. Because the expansive afforestation progressed from the lower reaches toward the upper reaches, the plantation stand age tends to be younger in the upper reaches than in the lower reaches. Thus, these physiographic and artificial factors along the lower–upper reaches gradient are closely connected to each other and affect the species composition of naturally regenerated trees, and each parameter may reflect the compound influence of the above-mentioned factors.

The results of the path analysis showed that the influences of previous forest type and geology were significant among factors that correlated with the species composition of naturally regenerated trees (Fig. 2). Also, the community types correspond to previous forest types, i.e., Type A1 (dominant species: *S. controversa*, etc.) and Type A2 (*B. maximowicziana*, etc.) to the *Thujopsis*, *Fagus*, *Aesculus* type, Type B1 (*Q. serrata* and *C. crenata*) to the *Quercus* type, and Type B2 (*P. densiflora*) to the *Pinus* type (Fig. 3). The species composition of naturally regenerated trees maintains the character of the composition of the previous forest or the surrounding natural forest because those trees originate from advanced seedlings, sprouts, or colonization through seed dispersal from surrounding stands (Kodani 2006; Utsugi et al. 2006). Thus, previous forest type directly affects the species composition of naturally regenerated trees in plantations, causing the greatest absolute value of the rank correlation coefficient and path coefficient. Variations in the species compositions of naturally regenerated trees in plantations depending on previous vegetation type have been reported between cases in which grassland and hardwood secondary forest were afforested (Ito et al. 2004), and between cases in which hardwood secondary forest and conifer plantation were afforested (Ito et al. 2003). The present study demonstrated that previous forest type differences also existed between primeval forest, which showed relatively little influence of artificial disturbances, and secondary forests, which showed large influences. However, not all of the components of previous forests occurred in subsequent plantations. For the *Thujopsis*, *Fagus*, *Aesculus* type, the dominant species of the previous natural forest scarcely occurred in plantations, while the dominant species of the previous secondary forest were abundantly found in the plantations for the *Quercus* type and the *Pinus* type (Table 1). This suggests that the ability to recover or colonize into plantations differs between species, especially between natural forest species and secondary forest species.

Some studies have pointed out variations in the species composition of naturally regenerated trees in plantations according to slope position (Kodani 1990; Hasegawa 1992). However, in the region surveyed in the present study, this difference was not significant except that the appearance of Type A1 showed bias toward the lower parts of the slopes (Fig. 3), and the path analysis did not indicate a significant relation (Fig. 2). Hasegawa and Taira (2000) also described no notable variations in the species composition of naturally regenerated trees in plantations depending on the slope position, although they pointed out that there was a significant variation for their previous forests. How the success of colonization depends on slope position differs according to tree species, and so the frequency and the relative dominance of each tree species should be compared between the previous forests and the plantations.

Factors affecting the abundance of naturally regenerated trees

All examined parameters except for slope aspect and stand age showed significant correlations with the relative basal area of naturally regenerated trees (Table 4). Among these, geology gave the greatest absolute value of the rank correlation coefficient (Table 4), although no effective models explaining the relative basal area of naturally regenerated trees were yielded by path analysis. *Cryptomeria japonica* plantations were remarkably unsuccessful on the dacitic tuff in the hilly areas of the lower reaches (Fig. 5), and colonizing *P. densiflora* trees suppressed planted *C. japonica* trees. This rock is relatively soft-sedimentary and is assumed to be permeable by water (Tada 1976). Such a geological property would produce a dry soil, and might hinder the growth of the planted *C. japonica* and facilitate the colonization of *P. densiflora*. The growth of *C. japonica* is significantly influenced by site productivity (Mashimo 1983). Because *P. densiflora* grows faster in terms of height and its growth does not drop as markedly with low site productivity as the growth of *C. japonica*, colonizing *P. densiflora* trees reach the canopy layer and suppress the planted *C. japonica*.

Some case studies have pointed out the effects of topographic conditions on the abundance of naturally regenerated trees in plantations; successful *C. japonica* plantations are located on broad ridges and smooth slopes, and unsuccessful hardwood-dominated plantations on narrow ridges and unforested areas in valleys (Maeda 1992), while unsuccessful *C. japonica* plantations with abundant naturally regenerated hardwoods are located on eastern slopes (Masaki et al. 2004). In the present study, slope aspect did not significantly correlate with the abundance of naturally regenerated trees (Table 4). The slope positions significantly correlated with the abundance of naturally regenerated trees (Table 4), with their values being remarkably high on flood plains in hilly areas (Fig. 5). However, variations with slope position were not significant in the mountainous areas, indicating that slope position does not affect the abundance of naturally regenerated trees as much as geology does.

The present study revealed the effects of previous forest types and geology on the occurrence of naturally regenerated trees in plantations. An examination of the mechanism associated with these factors would provide useful information for the management of plantations mixed with naturally regenerated trees.

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