Twenty-one Years Post-fire Succession in a Small Watershed on Etajima Island, Hiroshima Prefecture, Southwestern Japan

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Abstract

This study was conducted in a small watershed in Etajima Island, southwestern Japan to ascertain species performance 21 years after the fire using the Braun-Blanquet's method. Five plots were laid out in the burnt area for the interpretation of succession taking the edaphic or topographic conditions into consideration. Two fern species, *Gleichenia japonica* and *Dicrapnopteris dichotoma*, that grew from surviving subterranean organs a year after the fire helped much in the recovery of the vegetation. At the onset of succession, soil erosion was controlled and trees invasion prevented due to the rapid growth and distribution of these ferns. Vegetation growth showed variations as could be gleaned from the length of time when the shrub, sub tree and tree layers have pervaded the area. In 1996, the tree layer appeared in a NW-valley side slope (Plot 3) with *Pinus densiflora* enlarging its crown over other broad-leaved trees. *Clethra barbinervis*, on the other hand, started developing in the sub tree layer in the plot on valley bottom at lower slope (Plot 1), middle valley bottom slope (Plot 2), and NE-valley side slope (Plot 4) in 1980, 1989, and 1985, respectively. In 1990, *Pinus densiflora* developed in NW-valley side slope (Plot 3) and on the ridge plot (Plot 5). Shrub layer developed in all plots two years after the fire except the plot on the ridge (Plot 5) where shrub appeared after four years.

1. Introduction

Fire is one of the representative disturbances of forests in Japan. Studies done by Nakagoshi et al. (1987a) show that the country's forest is hit by fire on the average of 4,937 times annually. In 1985, the fires have destroyed about 5,149 ha of Japan's forests. However, unlike forest fires in other countries, almost all forest fires are caused by human activities. This could be gleaned from the data showing that forest fires have been frequented in such areas with high population density as Saitama, Chiba, Tokyo,

Kanagawa, Aichi, Osaka, Hyogo, Kagawa and Fukuoka. This phenomenon is similar in Canada. Data collated during the 1996 National Workshop on Wildland Fire Activity in Canada showed that the increasing population with easier and more frequent access to forest had increased fire activity in the region.

One of the big forest fires in the area was in Etajima Island on June 1, 1978. Today, like other Japan's forests struck by fire, Etajima is vegetated by young *Pinus densiflora* forest.

Studies on post-fire regeneration of forest vegetation in southern Hiroshima Prefecture have been conducted. For instance, Nakagoshi & Nehira (1982) examined the aspect of the controlled forests in the regeneration of vegetation in the burned pine forests in southern Hiroshima Prefecture. Nakagoshi et al. (1983b) also studied the post-fire regeneration of 21 years old stand in Otake, southwestern Japan. The above studies ascertained the cyclic regeneration of *Pinus densiflora* forests.

Follow-up surveys of post-fire succession two decades after the fire in Etajima Island have never been reported. This study was, therefore, conducted to clarify the prevailing post-fire regeneration pattern and dominance of pine forests and find out the relationship between life forms and the temporal and spatial distribution that result from vegetation change. The aspects of post-fire succession such as coverage, height distribution and diversity indices of vegetation are also reported.

2. Study Area and Methods

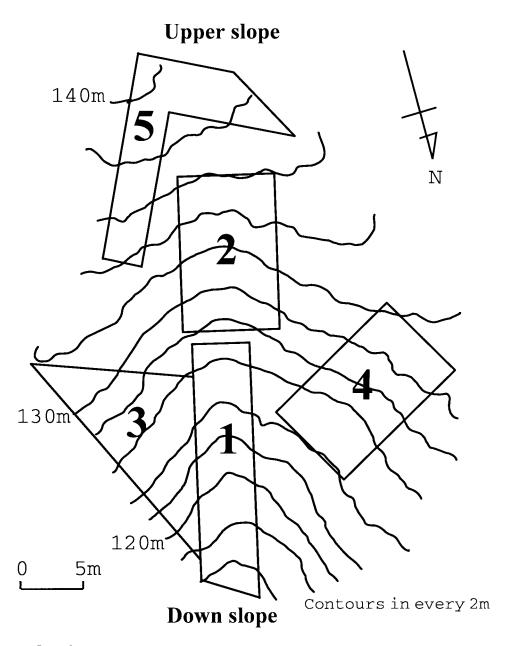
This study was conducted in Etajima Island, 8 km south of Hiroshima City. From the nearest meteorological station at Hiroshima, the mean annual temperature is 15.4 °C and the annual precipitation is 1608 mm (Anon.,1982). The climate is relatively dry with hot summers and the geological substrate is composed of highly weathered granite and rhyolite where the former vegetation before the fire was assumed to be the association of Rhododendro-reticulati-Pinetum densiflorae H. Suzuki et Toyohara 1971 (Nakagoshi et al., 1987a).

Five plots were laid out on a completely burnt slope at a valley head in the watershed area. Area of each plot was 100 m² (Nakagoshi et al., 1984). In the selection of the plots, microtopography was considered. Thus, the location of the plots were as follows: Plot 1, on the valley bottom at lower slope; Plot 2, on the middle valley bottom slope; Plot 3, facing the NW-valley side slope; Plot 4, facing the NE-side slope; and Plot 5, on the ridge (Fig. 1).

The physiognomical investigation using Braun-Blanquet's method was started from 1979 during spring of each year, and covered the 21-year post-fire succession. The Raunkier's life form system was used to further clarify the species composition consisting of such phanerophytes as mesophanerophytes (MM), microphanerophytes (M) and nanophanerophytes (N); and, herbaceous plants like hemicrypthophytes (H), geophytes (G) and therophytes (Th).

Mesophanerophytes are plants reaching the height of 5-30m; microphanerophytes, 2-5m and nanophanerophytes, <2m. Therophytes are annual or ephemeral plants that complete their life cycle rapidly during periods when conditions are favourable and survives unfavourable condition. Geophytes, on the other hand survive in unfavourable condition by means of underground food storage organs (e.g. rhizomes, tubers, and bulb) while hemicrypthophytes are plants whose perrenating buds are at ground level, the aerial shoots dying down at the onset of unfavourable condition (Mueller-Dombois & Ellenberg, 1974).

However, since there are no megaphanerophytes in Japan, the classification system evolved by Ito



Legend:

Plot 1 - a plot on the valley bottom at lower slope

Plot 2 - a plot on the middle valley bottom slope

Plot 3 - a plot facing NW-valley side slope

 ${\tt Plot~4-a~plot~facing~NE-valley~side~slope}$

Plot 5 - a plot on the ridge

Fig. 1. The established plots in the area.

(1977) was used: 1) mesophanerophytes (8-30m); 2) microphanerophytes (3-8m); and 3) nanophanerophytes (3m). In addition, plant species that assume different life forms when growing under different environmental conditions were classified as creeping mesophanerophytes (L(MM)) and creeping nanophanerophytes (L(N)). Mueller-Dombois & Ellenberg (1974) explained that certain high altitude tree species assume a creeping growth habit called "Krummholz", near their upper limit of distribution while they grow as perfectly normal trees below.

As the diversity index of vegetation, the Shannon-Wiener Index of diversity was calculated,

$$\underline{H}' = -\sum_{i=1}^{s} p_i \ln p_i,$$

where \underline{s} is the number of species; \underline{p}_i , the proportion of individuals or the abundance of the \underline{i} th species expressed as a proportion of total cover.

3. Results

3.1 Number of plant species

A total of 75 species of vascular plants appeared in the five plots throughout the 21-year post-fire succession. These plant species showed different responses to vegetation renewal as expressed in their species richness (Fig. 2). Most plant species appeared in the herb layer. In this layer, fluctuation in the

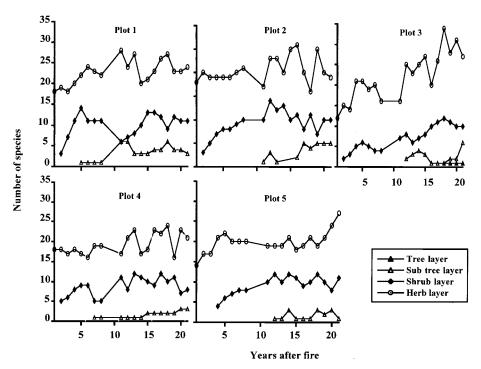


Fig. 2. Comparison of regenerated plant species in each plot.



Fig. 3 The number of plant species in each plot per year.

number of species was observed where most periodic decrease resulted to the increased number of species in the shrub layer. Similar pattern was manifested when the sub tree species started to establish in each plot reducing the number of species in the shrub layer. Most number of plant species in the herb, shrub and sub tree layers was abundant in Plot 1. Of all the plots, lowest number of species in the shrub layer occurred in Plot 3. However, when the tree layer appeared after 18 years in this plot, number of species in the herb layer increased as well as the shrub layer. Slow development took place in Plot 5; thus the number of sub tree layer was the least among the plots.

In general, plant species abundance was highest in Plot 1 (valley bottom at lower slope). This was followed by Plot 3 (facing NW- valley side slope), Plot 2 (middle valley bottom slope), Plot 4 (facing NE- valley side slope), and Plot 5 (on the ridge). However, 21 years after the fire, Plot 3 generated the most number of species. Plots 5, 1, 4, and 2 followed respectively.

During the initial post-fire stage, plant species were mostly found in Plots 1, 2, and 4, but were least observed in Plots 3 and 5 (Fig. 3). Plots 1 and 2 recovered fairly quickly compared to other plots during the first eight years of succession. The number of plant species in all plots increased and reached the peak four years after the fire. Afterwhich, the species richness gradually decreased within three years except in Plot 1 where it increased consistently until the sixth year. In Plot 3, number of species was the least among the plots 8 years after the fire, but this sped up 10 years after. During this period the young *Pinus* had already been established in the area (Fig. 6), resulting to the increase in the number of species in the herb and shrub layer species respectively (Fig. 2).

Figure 3 assumes the four stages of early successional process after disturbance in a post-fire stand. On the first year, recovery of vegetation would depend on the regulation of environmental conditions rather than community interaction system; primary disturbance stage. The gradual increase in the number of plant species after the disturbance could be attributed to the changes in environmental conditions

Table 1. List of lifeforms and their corresponding maximum dominance.

Tuble 1. Elst							· ~ F			,	Vacr									
Species	Life form	1979	1980	1981	1982	1983	1984	1985	1986	1989	Year 1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
Gleichenia japonica	G	2	2	3	4	3	3	1	3	4	4	4	5	5	5	5	5	5	5	4
Miscanthus sinensis	н	+	2	3	3	3	3	3	3	4	3	4	1	2	2	1	2	1	2	1
Dicranopteris dichotoma	G	1	1	1	1	1	1	1	1	2	2	2	2	2	1	3	3	3	2	3
Smilax china	L(N)	1	1	1	1	2	1	2	2	2	2	2	2	3	2	2	2	2	2	2
Eurya japonica	M	1	1	1	2	3	3	2	2	3	3	2	2	2	2	2	2	2	2	3
Clethra barbinervis	M	1	1	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2
Lyonia ovalifolia var. Elliptica Lespedeza cyrtobotrya	N	+	1	1	2	2	2	2	3	2	1	1	+	+	1	+	+	1	+	1
Wikstroemia sikokiana	N	+	+	1	2	2	2	2	2	2	1	1	1	1	1	1	2	1	1	2
Vaccinium oldhamii	N	+	+	+	1	2	2	2	2	2	1	1	1	1	1	1	2	1	1	2
Quercus serrata	MM	1	1	1	1	1	2	2	2	2	1	1	1	2	1	1	1	1	2	2
Rhododendron kaempferi	N	1	1	1	1	1	1	2	2	2	2	1	+	2	1	2	1	1	2	2
Ilex crenata	N	+	+	+	+	+	3	2	2	2	2	1	1	1	1	1	1	1	1	2
Viburnum wrightii	N	+	+	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Haloragis micrantha	н	+	+	1	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Abelia serrata	N N	+	+	+	1	1	+	2	1	1	1	2	+ 1	+	+	1	1	+	+	+
Rhododendron mucronulatum forma ciliatum Rhus trichocarpa	M	+	+	+	+	+	1	2	1	1	1	1	1	1	1	1	1	1	1	1
Pieris japonica	M	†	+	+	+	+	+	1	1	1	1	1	1	1	1	1	1		- !	+
Zanthoxylum schinifolium	N	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+	+	+	+
Mallotus japonicus	MM	+	+	+	+	+	+	+	+			+	+	+			+			+
Amelanchier asiatica	M	+	+	+	+	+	+	+	+			1		1		+	1_	1	1	1
Lysimachia clethroides	н	-	1	1	2	2	2	1	1	1	1	1	-		1	-	-	-	-	
Pinus densiflora	MM		+	+	1	1	2	1	1	2	1	2	1	2	2	2	2	3	3	3
Arundinella hirta	н		1	1	1	1	1	+	+	+	1	+	+	1	1	+	1	1	1	+
Pteridium aquilinum var. latiusculum	G		+_	+	+	+	+	+	+	1	+	1	+	+	+	+	+	1_	+	+
Aletris luteoviridis Solidagovirga-aurea var. asiatica	H H		•		+ +	+	+	1	1	1	1	+	+	+	+	1	1	1	1	+
Viola violacea	H		-		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Rhamnus crenata	N.	•		•	1 .	+	+	+	+	1	1	1	1	1	1	1	1	1	1	1
Alnus sieboldiana Matsum.	M	•		•	1	+	+	+	+	+	+	1	1	1	Ċ	1	1	2		2
Rhus javanica	M				1	+	+	+	2	+	+	+						-	+	+
Polygala japonica	Н				-		+			+		+	+	+	+		+	+	+	
Carex floribunda	н									+	+	+	+	+		+	+	+	+	+
Prunus jamasakura	MM									+	+	+	+		+	+	+	+	+	+
Rhododendron reticulatum	N				-					_1_	1	2	11	+	+	11	+			+
Juniperus rigida	М									٠ ا	+	+	+	+	+		1	1_	+	+
Acacia confusa Platanthera minor	M G												+	+		+	1	1	1 2	1
Ixeris dentata	Н	'	-							•			+			+	+		+	
Trachelospermum asiaticum var. intermedium	L(MM)	•		•		•		•	•			•	•			;	+			
Castanea crenata	MM															+			+	1
Heloniopsis orientalis	н																+	1		+
Viola mandshurica	н																			+
Vaccinium smallii var. glabrum	N																			+
Hydrangea luteo venosa	N				-															1
Vaccinium bracteatum	N Th	-	٠.																.	+
Erigeron sumatrensis Crassocephalum crepidioides	Th	1 +																		
Erechtites hieracifolia	Th	+	1 .							•			•							
Andropogon virginicus	н		+	<u> </u>	+			•	•			•	•			•	•			
Artemisia princeps	н		+	+	+	i i														
Deutzia crenata	N		-		+	+	+	+	+] .										
Sphenomeris chusana	н				+		+	+	+										+	
Swertia japonica	Th						+	+	+].,										
Rosa multiflora	N										+									
Rubus palmatus	N M									. [+	1	. 1	. 4	. 1	. 4	. 1			
Pourtiaea villosa var. laevis Silene firma	Th										٠ ا	_1_	_1_	1	+	1	1			
Viburnum erosum	N							•					•		‡	1:				
Cephalanthera falcata	G														<u> </u>			+		
Pourthiaea villosa	М																.	_1		
Albizia julibrissin	M																. '		+	
Others																				
Rubus microphyllus	N	+	+	+	+	+	+	+	+	+	+									
Lespedeza bicolor forma. acutifolia	N		+	+	+	1	1													
Carex stenostachys	H				+	+	+				+	+	+	+	+	+	+	+		
Vaccinium japonicum Struthiopteris niponica	N H									1	1	. 2		1						
Strutniopteris niponica Digitaria adscendens	H Th					•	•			- 1	+	4			•	•				
Michella undolata	н							•			Ť.		+		+		+		:	
Sarothamnus scoparius	N.							+		:					+			+		
Viburnum dilatatum	N														2	1				
Carex conica	н																1	1		
Ophiopogon japonicus	н												+						+	
Akebia trifoliata	L(N)								+							+				
Total		27	30	30	37	36	39	37	37	36	40	41	40	39	40	40	43	42	40	41

Total

Legend:

MM - Mesophanerophytes

M - Microphanerophytes

N - Nanophaneophytes

H - Hemicrypthophytes

G - Geophytes

Th - Therophytes

L (MM) - creeping Mesophanerophytes

L (N) - creeping Nanophanerophytes

(e.g. direct insolation, soil temperature, moisture, nutrient resource etc.) affecting vegetation growth; degrading stage. The third phase is the recovering stage where shrub layer develops as post-fire succession progress and finally the secondary pine forest stage, when a secondary pine forest develops (Nakagoshi & Touyama, 1995).

Species composition after the fire consisted of 27 plant species (Table 1). Three life forms of herbaceous plants were found to inhere in this period as follows: *Erigeron sumatrensis, Crassocephalum crepidioides, Erechtites hieracifolia,* therophytes (Th); *Gleichenia japonica* and *Dicrapnopteris dichotoma,* geophytes (G); and, *Miscanthus sinensis, Haloragis micrantha* and *Platanthera minor*, hemicyrpthophytes (H). All these plant species were located throughout the 21-year post-fire succession except for *Platanthera minor* whose growth was limited and re-appeared after 14 years. The three therophytes were eliminated after a year.

There were 16 woody species that regenerated after the fire and persisted for 21 years. Of these, nine are nanophanerophytes (N) such as Lespedeza cyrtobotrya, Wikstroemia sikokiana, Vaccinium oldhamii, Rhododendron kaempferi, Ilex crenata, Viburnum wrightii, Abelia serrata, Rhododendron mucronulatum forma ciliatum and Zanthoxylum schinifolium. Microphanerophytes (M) like Eurya japonica, Clethra barbinervis, Lyonia ovalifolia var. elliptica, Rhus trichocarpa, and Pieris japonica also appeared. The mesophanerophytes (MM), Quercus serrata and creeping nanophanerophytes (L(N)), Smilax china formed part of the species that were present throughout the 21-year post-fire succession.

Some other woody species like *Mallotus japonicus* (MM) and *Amelanchier asiatica* (M) also appeared a year after the fire. Their growth were limited 11 years after the fire, thus they appeared and disappeared in the succession years just like *Rubus microphyllus* (N).

Two years after the fire, seven newly established plants were found to exist. Most of them were herbaceous plants such as Lysimachia clethroides, Arundinella hirta, Andropogon virginicus, and Artemisia princeps, hemicrypthophytes; and Pteridium aquilinum var. latiusculum, a geophyte. Pinus densiflora (MM) and Lespedeza bicolor forma acutifolia (N) were also present in this phase of succession. Among these plant species Pinus densiflora, Arundinella hirta and Pteridium aquilinum var. latiusculum appeared consistently in the area. Lysimachia clethroides established well for 13 years and appeared once afterwards. The growth of Lespedeza bicolor forma acutifolia was also limited after six years.

No newly established plants were observed after three years. However, after four to eight years of succession, 11 new plant species were located. On the fourth year, the following species were found to exist: Aletris luteoviridis, Solidago virga-aurea var. asiatica, Viola violacea, Sphenomeris chusana and Carex stenostachys, hemicrypthophytes; Rhus javanica, mesophanerophytes; and Deutzia crenata, nanophanerophytes. In addition, Rhamnus crenata (N) and Alnus sieboldiana Matsum. (M) appeared on the fifth year, and Swertia japonica (Th) on the sixth year.

Among these plant species, Aletris luteoviridis, Solidago virga-aurea var. asiatica and Rhamnus crenata persisted until 21 years. On the other hand, Viola violacea, Alnus sieboldiana Matsum., Rhus javanica, and Carex stenostachys showed some years of non-existence in the successional pathway while total elimination of Swertia japonica occurred after three years.

Some other species like *Sarothamnus scoparius* (N) and *Akebia trifoliata* (L (N)) established after seven and eight years respectively. These plant species did not show consistent emergence throughout the 21-year post-fire succession.

Hemicrypthophytes were the most common life forms that formed during the first eight years of suc-

cession and co-existed with other pioneer species that persisted throughout the 21-year post-fire succession. After 11 years and onwards, newly established plants showed a different pattern of life-form establishment. The number of herbaceous plants invading reduced and favorable establishment for woody species occurred.

Newly invading plant species after 11 years were as follows: *Polygala japonica* (H), *Carex floribunda* (H), *Struthiopteris niponica* (H), *Prunus jamasakura* (MM), and *Rhododendron reticulatum* (N). After 12 years, *Juniperus rigida* (M), *Rosa multiflora* (N), *Rubus palmatus* (N), and *Digitaria adscendens* (Th) pervaded the area. *Pourtiaea villosa* var. *laevis* (M) existed after 13 years while *Acacia confusa* (M) and *Michella undolata* (H) after 14 years. Plant species that established in these years showed inconsistent growth development, thus they were not found in some periods. Apparently, *Rosa multiflora* and *Rubus palmatus* were eliminated after a year of their growth.

Vaccinium japonicum (N) was the lone newly established plant after 15 years among other species. The succeeding year showed the presence of Silene firma (Th), Viburnum erosum (N), Viburnum dilatum (N), and re-appearance of Sarothamnus scoparius (N). The survival of these plant species were limited in some years, hence they were not found all through the years on their establishment.

Towards the end of the succession period being observed, 12 new plant species existed. After 17 years, *Ixeris dentata* (H), *Trachelospermum asiaticum* var. *intermedium*, a creeping mesophanerophyte (L(MM), and *Castanea crenata* (MM) started to appear in the site. Likewise, *Heloniopsis orientalis* (H) and *Carex conica* were found to exist after 18 years. The existence of *Cephalanthera falcata* (G), and *Pourthiaea villosa* (M) occurred 19 years after, while *Albizia julibrissin* (M) occurred 20 years after. At the year-end of the succession period, the following newly established plants appeared: *Viola mandshurica* (H), *Vaccinium smallii* var. *glabrum* (N), *Hydrangea luteo venosa* (N), and *Vaccinium bracteatum* (N).

3.2 Cover

Herbaceous vegetation established first in all plots with varying degrees of coverage. The highest was in Plot 1 (27%) and the least was in Plot 3 (8%; Fig. 4). Through the years herbaceous vegetation grew in profusion and consistently maintained its high coverage in Plots 1, 3, and 5. In Plots 2 and 4, the shrub layer coverage outnumbered the herb layer after seven years in 1 and 4-year period in the following order: 1986 (60%), Plot 1; and 1986 (55%), 1989 (75%), 1991 (70%), and 1992 (40%) in Plot 4.

Main herbaceous plants that grew a year after the fire were Gleichenia japonica, Dicrapnopteris dichotoma, Miscanthus sinensis, Crassocephalum crepidioides, Haloragis micrantha, Platanthera minor, Erigeron sumatrensis, and Erechtites hieracifolia (Fig. 5).

Two years after the fire, the shrub layer started to develop in Plots 1, 2, 3, and 4. In Plot 5, shrub layer began developing four years after. High coverage was in Plot 1 (8%) and the lowest was in Plot 3 (2%). When shrubs established four years after in Plot 5, it generated a high cover value (10%) compared to the earlier coverage in four plots. The coverage increased remarkably in Plots 1, 2, and 3 with 75%, 55%, and 35% coverage respectively after five years. In Plot 4, 45% coverage was recorded after four years. Also, the coverage in this plot continued to increase 8 to 11 years compared to Plots 1, 2, and 3 where abrupt decrease in the shrub coverage occurred after 8 years. In Plot 5, shrub development was slow, but after 12 years the coverage was high and increased fluctuatingly which generated the highest coverage (60%) among the plots after 21 years. On the contrary, Plot 2 had the least shrub layer cover-

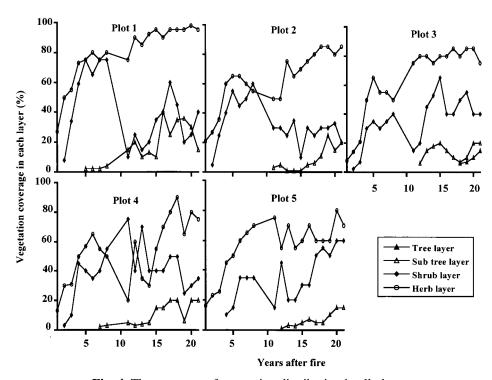


Fig. 4 The coverage of vegetation distribution in all plots.

age after the period of succession. Plot 4 followed. Plots 1 and 3 had equal coverage. The species composition in the shrub layer were as follows: *Pinus densiflora*, *Clethra barbinervis*, *Wikstroemia sikokiana*, *Eurya japonica*, *Quercus serrata*, *Lyonia ovalifolia* var. *elliptica*, *Rhododendron kaempferi*, *Rhus javanica*, *Vaccinium oldhamii*, *Mallotus japonicus*, *Rhus trichocarpa*, *Pieris japonica*, *Abelia serrata*, *Hydrangea luteo venosa*, *Lespedeza cyrtobotrya*, *Acacia confusa*, *Amelanchier asiatica*, and *Rhamnus crenata* (Table 2).

When the sub tree layer was already located in the site, the coverage of the shrub layer was affected, causing a reduction in coverage. Advanced vegetation development occurred always in Plot 1, thus the sub tree layer coverage was high and eventually generated the highest coverage after 16 years but the least in 21 years. In Plot 3, despite the delayed establishment of *Pinus densiflora* and *Lyonia ovalifolia* var. *elliptica* in this layer, the coverage developed progressively that after 15 years the cover value was high compared to Plots 1, 4 and 2 where *Clethra barbinervis* first located in 1983, 1985 and 1989, respectively. Coverage development of sub tree layer in Plot 5 progressed with time where the main species in the successional years was *Pinus densiflora* and some periodic appearance of *Clethra barbinervis* and *Quercus serrata*.

The coverage of tree layer started to develop after 18 years where *Pinus* generated a 15% cover value after 21 years.

Two fern species, *Gleichenia japonica* and *Dicrapnopteris dichotoma*, were responsible for the rapid recovery of the vegetation. Among the herbaceous plants, *Gleichenia japonica* was the most dominant, especially in Plot 1. This fern was observed in all plots except in Plot 5, which took five years before it

Plot 1 Plot 2 Plot 3 Plot 4 Plot 5 Tree layer Pinus densiflora Pinus densiflora Clethra barbinervis Pinus densiflora Clethra barbinervis Lyonia ovalifolia Clethra barbinervis Viburnum wrightii var. elliptica Pinus densiflora Lyonia ovalifolia Sub tree layer Lyonia ovalifolia Viburnum wrightii Clethra barbinervis Pinus densiflora var. elliptica var. elliptica Amelanchier Rhamnus crenata Rhus trichocarpa asiatica Quercus serrata Alnus sieboldiana Matsum. Pinus densiflora Pinus densiflora Pinus densiflora Eurya japonica Eurya japonica Clethra Clethra harhinervis Smilax china Smilax china barbinervis Wikstroemia Vaccinium Pinus densiflora Quercus serrata Eurya japonica sikokiana oldhamii Smilax china Vaccinium Quercus serrata Lyonia ovalifolia Eurya japonica Vaccinium oldhamii oldhamii Rhus trichocarpa var. elliptica Ouercus serrata Rhododendron Wikstroemia Wikstroemia Lyonia ovalifolia Hydrangea luteo Shrub layer Lyonia ovalifolia sikokiana sikokiana var. elliptica venosa Amelanchier var. elliptica Smilax china Rhododendron Wikstroemia Rhus trichocarpa asiatica Rhododendron kaempferi sikokiana Pieris japonica Rhodendron kaempferi Smilax china Lespedeza Abelia serrata kaempferi Rhamnus crenata Rhus javanica cytrtobotrya Lyonia ovalifolia Lyonia ovalifolia Vaccinium oldhamii Acacia confusa var. elliptica var. elliptica Mallotus japonicus Thus thrichocarpa Castanea crenata Gleichenia japonica Gleichenia Dicrtapnopteris Gleichenia iaponica dichotoma japonica Dicrapnopteris Gleichenia Platanthera minor Gleichenia Dicrapnopteris dichotoma Pteridium iaponica japonica dichotoma Pteridium Dicrapnopteris aquilinum var. Dicrapnopteris Heloniopsis aquilinum var. dichotoma latiusculum dichotoma orientalis latiusculum Aletris luteoiridis Miscanthus Herb layer Platanthera minor Miscanthus sinensis Miscanthus Miscanthus sinensis Miscanthus sinensis Carex floribunda sinensis sinensis Aletris luteoviridis Aletris luteoviridis Solidago virga-Haloragis Haloragis Haloragis Haloragis aurea var. micrantha micrantha micrantha micrantha Aletris luteoviridis Carex floribunda asiatica Solidago virga-Alletris luteoviridis Viola mandshurica aurea var. Crex floribunda asiatica

Table 2. List of plant species in each layer after 21 years.

established. Both Gleichenia japonica and Dicrapnopteris dichotoma grew rapidly from their subterranean organs. Their abundance prevented soil erosion on the bare substrate damaged by fire but also contributed in the delayed development of tree layer in addition to the competition effect posed by the sub tree layer in Plot 1 (Fig. 5).

Arundinella hirta

3.3 Structural Development

					3
Layer	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Tree layer			Pinus densiflora (1996)		
Sub tree layer	Clethra barbinervis (1983)	Clethra barbinervis (1989)	Pinus densiflora Lyonia ovalifolia var. elliptica (1990)	Clethra barbinervis (1985)	Pinus densiflora (1990)
Shrub layer	Clethra barbinervis Eurya japonica Viburnum wrightii (1980)	Clethra barbinervis Lespedeza cyrtobotrya Quercus serrata (1980)	Lespedeza cyrtobotrya Vaccinium oldhamii (1980)	Eurya japonica Lespedeza cyrtobotrya Quercus serrata Rhododendron kaempferi (1980)	Eurya japonica Lyonia ovalifolia var. elliptica Quercus serrata Wikstoemia sikokiana (1982)
Herb layer	Gleichenia japonica Dicrapnopteris dichotoma Miscanthus sinensis Crassocephalum crepidioides Haloragis micrantha Platanthera minor (1979)	Gleichenia japonica Dicrapnopteris dichotoma Miscanthus sinensis Erigeron sumatrensis Erechtites hieracifolia Haloragis micrantha (1979)	Gleichenia japonica Dicrapnopteris dichotoma Miscanthus sinensis Erigeron sumatrensis Crassocephalum crepidioides Haloragis micrantha (1979)	Gleichenia japonica Dicrapnopteris dichotoma Miscanthus sinensis Erigeron sumatrensis Crassocephalum crepidioides Haloragis micrantha (1979)	Dicrapnopteris dichotoma Miscanthus sinensis Erigeron sumatrensis Crassocephalum crepidioides Haloragis micrantha (1979)

Fig. 5 The period of vertical structure development in the studied plots.

The vertical structure of recovering vegetation progressed with time, in which development headmost in Plot 1. Plots 4, 2, 3 and 5 followed through. Figure 6 shows that height change from herb to tree layer was distinct in Plot 3.

In the herb layer, the least number of species were shown in Plot 5 while the other plots had the same number of species (Fig. 5). Of these, *Dicrapnopteris dichotoma*, *Miscanthus sinensis*, and *Haloragis micrantha* were common in all plots while *Platanthera minor* and *Erechtites hieracifolia* appeared only in Plots 1 and 2 respectively. In every plot, shrub layer appeared almost simultaneously in the early 1980's. However, there were differences in dominant species among the plots: *Clethra barbinervis*, *Eurya japonica*, and *Viburnum wrigthii* in Plot 1; *Clethra barbinervis*, *Lespedeza cyrtobotrya* and *Quercus serrata*, Plot 2; *Lespedeza cyrtobotrya* and *Vaccinium oldhamii*, Plot 3; *Eurya japonica*, *Lespedeza cyrtobotrya*, *Quercus serrata*, and *Rhododendron kaempferi*, Plot 4; and *Eurya japonica*, *Lyonia ovalifolia* var. *elliptica*, *Quercus serrata* and *Wikstroemia sikokiana*, Plot 5 (Fig. 5). The years indicated in the figure were the period when these plant species first appeared in the different layers of vegetation.

Figure 5 also shows that *Lespedeza cyrtobotrya* and *Quercus serrata* appeared in three plots compared to other early species in the shrub layer. As succession progressed, the presence of *Lespedeza cyrtobotrya*, nanophanerophytes and the mesophanerophytes, *Mallotus japonicus* were visible in the area especially during the first eight years after the fire (Figure 7). Although, *Mallotus japonicus* has low frequency distribution and concentrated mainly in Plot 1, its visibility was apparent as affected by rapid

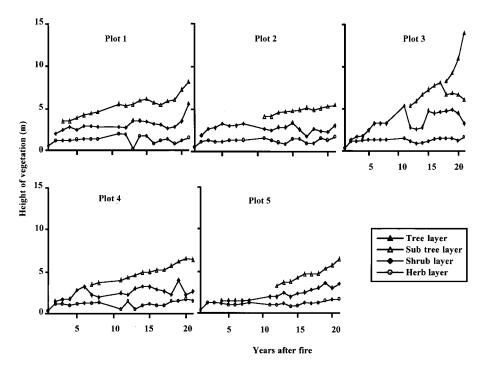


Fig. 6 The height distribution in all plots.

coverage and height development in this plot. In this period of succession, *Pinus densiflora* was already located but the abundance was not yet evident not until 12 years after the fire. The frequency distribution of the pine in the area tremendously increased together with *Rhododendron* spp., of which *Rhododendron kaempferi* was prominent among the three species of *Rhododendron* that were located. The presence of *Rhododendron reticulatum* became visible in the area after 11 years (Table 1).

The height of sub tree layer in Plot 2 was the least developed among the plots. Since most plant species in the sub tree layer appeared in this plot next to Plot 1, competition impeded its height development (Figure 2). This pattern was similar in Plot 1 where height development was delayed because of sudden increase of shrub layer's composition 11 years after the fire (Fig. 2). However, when the number of species in the shrub layer was reduced, remarkable increase in the height of sub tree layer was manifested after 18 years in Plot 1.

After 21 years, main species in the sub tree layer were *Pinus densiflora*, *Clethra barbinervis*, *Viburnum wrightii*, *Lyonia ovalifolia* var. *elliptica*, *Rhus trichocarpa*, *Quercus serrata*, *Amelanchier asiatica*, *Alnus sieboldiana Matsum.*, and *Rhamnus crenata* (Table 2). *Pinus* reached the height of 14 m after 21 years in Plot 3.

3.4 Life forms

Using Raunkiaer's life form system, eight life forms were identified among the regenerated plant species. These included phanerophytes such as mesophanerophytes (5 spp.), microphanerophytes (13

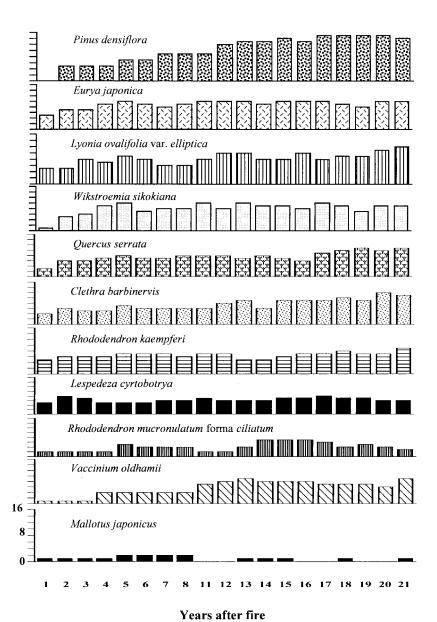


Fig. 7 The frequency distribution of major phanerophytes in successional years.

spp.), and nanophanerophytes (23 spp.), and herbaceous plants such as hemicrypthophytes (20 spp.), geophytes (5 spp.), and therophytes (6 spp.). Two creeping phanerophytes that assume the height of mesophanerophytes (1 spp., i.e. *Trachelospermum asiaticum* var. *intermedium*) and nanophanerophytes (2 spp., i.e. *Smilax china* and *Akebia trifoliata*) were found to exist.

A year after the fire, 27 individual plant species were identified and represented the following group of life forms: mesophanerophytes (7.4%), microphanerophytes (22.2%), nanophanerphytes (37.04%),

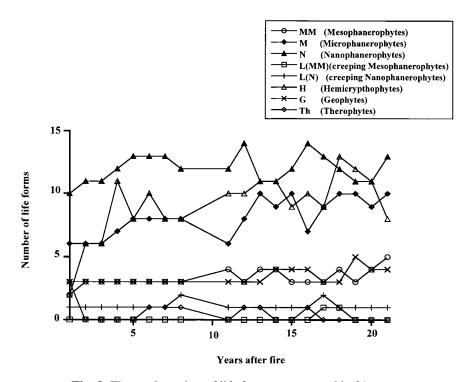


Fig. 8 The total number of life forms regenerated in 21 years.

hemicrypthophytes (7.4%), geophytes (11.1%), therophytes (11.1%), and creeping nanophanerophytes (3.7%). Their growth pattern implied that most plants a year after the fire grew from coppices, subterranean organs and from new invading seeds as exhibited by *Erechtites hieracifolia*, *Erigeron sumatrensis*, and *Crassocephalum crepidioides*.

The appearance of woody plants such as nanophanerophytes and microphanerophytes are comparable to herbaceous plants such as hemicrypthophytes, geophytes, and therophytes (Fig. 8). The number of nanophanerophytes was consistently high 17 years after the fire. Hemicrypthophytes increased tremendously after four years and outnumbered the nanophanerophytes in 2-year period, 18 and 19 years after the fire. On the other hand, microphanerophytes started to increase four years after the fire and outgrew the hemicrypthophytes after 15 years. Mesophanerophytes and geophytes constantly kept almost a constant number and periodically increased and decreased after 11 years. The creeping nanophanerophytes represented by *Smilax china* and *Akebia trifoliata* showed the persistence of the former species throughout the 21-year post-fire succession while the latter appeared only twice. The creeping mesophanerophyes appeared only once. Therophytes generated the least number of life forms among the herbaceous plants. During the first 8 years of succession newly established plants were mostly hemicrypthophytes. However, 11 years after and onwards, increased emergence of woody species occurred.

Table 1 shows the appearance of plant species in the successional pathway according to their life forms and their corresponding maximum dominance. It shows that 29.0% of the 75 plant species have existed through the 21-year post-fire succession. Herbaceous plants such as geophytes and hemicryptho-

phytes were able to co-exist with the group of phanerophytes that showed uninterrupted growth throughout the period of succession. Of these, *Gleichenia japonica* reached the maximum dominance that started 14 years after the fire. On the other hand, among the phanerophytes, the mesophanerophytes *Pinus densiflora* developed and reached the tree layer after 18 years.

Pinus densiflora has winged dispersible seed, and due to its accelerated growth it generated the highest cover value among the other broad-leaved trees. Some other plant species that showed high cover values were as follows: Quercus serrata, Eurya japonica, Lyonia ovalifolia var. elliptica, Clethra barbinervis, Wikstroemia sikokiana, Rhododendron kaempferi, Lespedeza cyrtobotrya, Vaccinium oldhamii and Smilax china. These species have shown their dominance in the 21-year post fire succession (Table 1).

3.5 Diversity Index

Diversity index showed that the herb layer was the most diverse layer in most plots especially in Plot 5 and least in Plot 1 (Fig. 9). In contrast, high diversity index in the sub-tree layer was observed in Plot 1, while lowest in Plot 5. Herb layer diversity index was sustained to be high where the development of the shrub layer was slow. The shrub layer diversity index after 4 years in Plots 1 and 2 was high but discrete shrub diversity index was shown in Plot 1 for 5 consecutive periods after 3 years. Herb layer diversity index remained to be high in Plots 2, 4 and 5 although there were periodic increase in the shrub

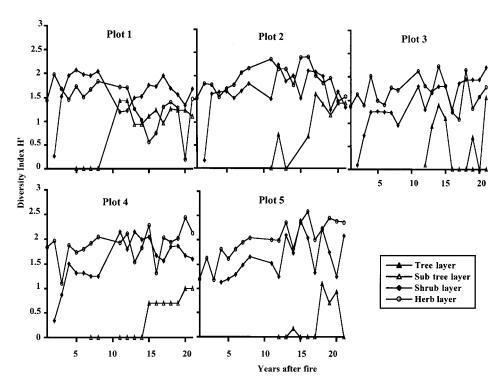


Fig. 9 Diversity index in each layer per plot.

diversity indices especially in Plot 4. After 21 years, the shrub layer diversity was high in Plots 1 and 3.

In the shrub layer, Plot 2 was the most diverse among the plots, while Plot 5, the least diverse. Since the middle of the slope followed always Plot 1 in vegetation development, shrub layers were conspicuous in the middle valley bottom slope. However, compared to Plots 2 and 4, Plot 3 had the least shrub layer diversity among the plots in the middle valley bottom slope.

The sub tree layer diversity index became visible after 11 years onward in most plots but foremost in Plot 1. This plot on the lower valley bottom at lower slope exceeded the shrub's diversity index in 2 years. The indices in Plots 2 and 4 showed an increasing fluctuation. The sub tree diversity indices in Plots 3 and 5 did not consistently develop. Apparently, diversity index in the tree layer was not expressed because only pines were visible in this layer.

In general, the diversity index in all plots increased after the fire. The rise and fall in the index were due to the growth, development and transition as well as competition of the life forms in the successional pathway causing mostly the elimination of the herbaceous plants.

Discussion

In the early stage of succession, annual weeds such as *Crassocephalum crepidioides*, *Erigeron sumatrensis* and *Erechtites hieracifolia* were first observed. According to Nakagoshi et al. (1983a) and Ohtsuka (1999) these therophytes are typical communities after a forest fire and establish well in the disturbed mountainous sites of temperate regions especially in clear felled forests.

Two years after the fire, these annual plants disappeared in the successional pathway. According to Bergon et al. (1990), early successional plants have fugitive lifestyle and their continued survival depend on dispersal to other disturbed sites. In addition, they cannot persist in competition with later species. Thus, they must grow and consume the available resources rapidly.

Aside from these therophytes, other herbaceous plants such as hemicrypthophytes and geophytes also facilitated the early vegetation recovery. Geophytes such as *Gleichenia japonica*, *Dicrapnopteris dichotoma* and *Pteridium aquilinum* var. *latiusculum* showed preponderant growth at the onset of succession, preventing rapid soil erosion. These fern species show renewal from their subterranean organs (Nakagoshi et al., 1987a) and their distribution could control the soil erosion after biomass destruction caused by the fire (Chinen & Hori, 1983). Data also show that the ferns' abundance in addition to competition effect of the recurring vegetation prevented the invasion of other trees especially in Plot 1. This is because they could suppress woody seedlings through their extensive and lateral spread above and below the ground. Although vegetation development was always advanced in this plot, no plant species reached the tree layer after 21 years. This conforms to the observation of Grime (1987) that in the presence of dominant herbaceous plants, invasion of trees could be inhibited because of their profound growth and development.

Bazzaz (1990) made a generalized pattern of dominance during succession field in temperate forest of eastern North America in which he pointed out those annual plants either winter annuals or summer annuals dominate on the first year (e.g *Erigeron canadensis*, *Erigeron annuus*, *Ambrosia artemiifolia*). On the second year, short-lived perennial herbs dominate that may actually recruit during the first year, but become prominent only in the second year because of their relatively slow growth rate (e.g. *Aster pilosus*). In addition he said that clonal herbs that can endure for several years constituted the third phase of recovery (e. g. genus *Solidago*, *Andropogon virginicus* for common grass). In the mid-succes-

sional fields he cited that common shrubs include the genera of *Rhus* and *Rubus* while early-successional trees include the evergreen *Juniperus* and *Pinus*. Various combinations of tree species could be found in late-successional habitats where he included *Acer*, *Fagus*, and *Quercus* among others.

These phases of succession somewhat corresponded the vegetation recovery in the studied plots in Etajima Island. When Crassocephalum crepidioides, Erechtites hieracifolia, and Erigeron sumatrensis diminished, the hemicryphytes Andropogon virginus and Artemisia princeps were located in the site for three years. On the other hand, the hemicrypthophytes Miscanthus sinensis, Haloragis micrantha and Arundinella hirta and the geophytes Gleichenia japonica, Dicrapnopteris dichotoma, and Pteridium aquilinum var. latiusculum persisted in the observed succession period. The time period when Solidago-aurea var. asiatica was founded and the presence of Andropogon virginicus occurred also when the third group of plant species have established in the area. Similarly, Rhus trichocarpa and Rhubus palmatus were also located among the plant species that regenerated after the fire where the former species was one among the 20 plant species that appeared throughout the 21-year post-fire succession. Significantly, the emergence of Pinus in the tree layer highlights the fact that early-successional trees of disturbance origin could tolerate some degree of limitation of soil moisture and nutrients, conditions that are characteristic of open, sunny habitat (Bazzaz, 1990).

The pattern of vegetation change in Etajima followed the cyclic regeneration pattern of *Pinus densiflora* forests in the Seto Inland Sea region. The community following the association of Crassocephalo crepidioidis-Erechtitetum hieracifoliae was the *Lespedeza cyrtobotrya* - *Mallotus japonicus* community. After eight years, the scrub of these plant species was already established in the site (Figure 7). The reason for this could be the fact that the seeds of *Mallotus japonicus* and *Lespedeza cyrtobotyra* are kept dormant and buried in the soil and are stimulated to germinate by fires. Thus, among the nanophanerophytes, *Lespedeza cyrtobotrya* showed high dominance along with *Wikstroemia sikokiana*, *Rhododendron kaempferi* and *Vaccinium oldhamii*. As a result, two years after the fire *Lezpedeza cyrtobotrya* and *Vaccinium olhamii* were visible in the shrub layer in Plot 3 (Fig. 5).

The successional pattern of the total number of species showed an increasing and decreasing trend for the first 10 years, followed by fluctuation about a mean (Fig. 3). The species richness in each plot did not show much difference after 10 years. The increase could be due to environmental and nutritional changes caused by the disturbance, while the decrease could have been due to such environmental conditions as climatic, topographic and edaphic factors (Nakagoshi & Touyama, 1995).

Pinus densiflora and Rhododendron spp. already appeared during the first 8 years except for Rhododendron reticulatum (Fig. 7), and in 1986, decrease in species richness was observed in most plots especially in Plot 3 where the least number of regenerated species occurred (Fig. 3). In this period, the coverage of the shrub layer in most plots were high especially in Plots 2 and 4 where shrub layer coverage surpassed the herb layer coverage (Fig. 4). This matched the observation of Nakagoshi & Touyama (1995) that change in vegetation and the development of shrub layer enhances competition for light, a factor detrimental to shade-tolerant species. Another implication in the decline of number of species was due to the non-establishment of newly invading plant species in this period except for the establishment of Akebia trifoliata, a creeping nanophanerophytes (Table 1). This observation corroborated with the findings of Rim et al. (1991) that chemical substances especially that of leaf extract and root extract of Pinus densiflora could inhibit the germination of weeds.

The period when the shrub and sub tree layer first established in each plot revealed that *Pinus* was comparatively late when it established in Plots 3 and 5 (Fig. 5). Despite the late establishment in the

area, tree layer coverage and height developed compared to the earlier broad-leaved trees. This suggests the fact that pines require bare mineral soil for germination and adapted to full sunlight (Kamada & Nakagoshi, 1991). In retrospect, it also highlights the susceptibility of pine forests to disturbance such as fire and their occurrence on nutrient deficient soils (Knight, 1991). In addition, Nakagoshi et al. (1987a), assumed that the former vegetation in Etajima before the fire was the association of Rhododendro-reticulati-Pinetum densiflorae, which is distributed in the western Seto Inland Sea Region. Three species of *Rhododendron* in site were present in the successional years that was observed, and *Rhododendron reticulatum* found to exist when young pines started to show their dominance in the area.

The post-fire succession pattern of plant communities in the study site was similar to that Seto Inland Sea region (Nakagoshi et al., 1987a). The pattern was: Crassocephalum - Erechtites community \rightarrow Lespedeza cyrtobotrya - Mallotus japonicus community \rightarrow Pinus - Rhododendron spp. communities. This, therefore, means that there was no temporal variation in the cyclic regeneration of pine forests in the Seto Inland Sea region two decades after the fire.

The established plots showed different responses to the growth of the recovering vegetation. The spatial distribution of regenerated vegetation was affected by microtopography based on the species richness regenerated in each plot (Fig. 2). Also, it took different length of time when vertical structure development had occurred (Fig. 5).

The rapid vegetation development observed in Plot 1 could be accounted for the filling up of organic material and water run-off along the slope that are useful for plant growth. This accorded the observation of Nakagoshi et al. (1987) that phytocoenoses development is always advanced in the valley bottom slope, followed by the valley slope (lower, mid and upper) and on the ridge. Nagamatsu & Miura (1997) explained that soil disturbance regime, environmental conditions such as moisture, soil nutrients, and light intensity may vary along micro-landform units and these factors would also affect the vegetation patterns. Hence, these factors could explain why vegetation progression best developed at the lowest portion of the slope, then at middle valley slope and last on the ridge.

The emerging pine forest affected the elimination of life forms like therophytes and creeping mesophanerophytes due to competition effect. Therophytes did not establish very well since they rapidly disappeared when large perennial plants were already established in the area. Thus, when the shrub layer and tree layers developed these woody plants replaced the herbaceous vegetation.

Diversity also increased along the 21-year post-fire succession although there were fluctuations due to vertical structure and growth development on the life forms present. Nakagoshi & Touyama (1995) reported that in general, post-disturbance vegetation may increase in diversity for a certain period, and afterwards intensified competition leads to a decrease in diversity.

The effect of the fire in the island must have been so extensive that evergreen broad-leaved trees did not appear in the successional pathway. According to Nakagoshi et al. (1987a), the Inland Sea region had evergreen oak forest as the climatic climax forest 3,000 years ago. This highlights the fact that disturbances such as fire and anthropogenic activities transform vegetation, which in turn create a pattern for the cyclic regeneration of pines. However, in Kanto district and central Hiroshima Prefecture, studies (e.g. Goto et al., 1996; Hong, 1995) showed that once management was neglected and pine forest were abandoned, broad-leaved trees and deciduous oak forest have replaced the dominant pine forests.

This study reveals that temporal variation do not affect the prevailing dominance of *Pinus densiflora* as a secondary forest in southwestern Japan. Although the forest is still in its early stage of succession, the young pine forest is able to change its understorey flora within 20 years. This result validates the

estimation of Nakagoshi & Nehira (1982) that vegetation in a regenerated pine forest can be developed within 20 years and confirms the observation of Bazzaz (1990) that *Pinus* among others is one of the early-successional tree species after disturbance similar to temperate forests of eastern North America.

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References

- [1] Anon. (1982), *The monthly normals of temperature and precipitation at climatological stations in Japan* (1951-1978). Technical Data Series No. 46. 216 pp. Japan Meteorological Agency, Tokyo (in Japanese).
- [2] Bazzaz, F. A. (1996), Plants in changing environment linking physiological population and community ecology. 320pp. Cambridge Univ. Press.
- [3] Bergon, M., Harper, J. L., and Townsend C. R. (1990), Ecology Individuals, Populations and Communities. 2nd ed. 945pp. Blackwell Scientific Publications.
- [4] Burrows, C. J. 1990. Process of vegetation change. 551pp. Unwin Hyman, London.
- [5] Chinen, T. and Hori, N. (1983), Observation of slope erosion processes after a forest fire, Etajima Island. Memoirs of Faculty of Integrated Arts and Science, Hiroshima University Series IV, 8:127–155 (in Japanese with English summary).
- [6] Goto, Y., Yoshitake, T., Okano, M., & Shimada, K. (1996), Seedling regeneration and vegetative resprouting after fires in *Pinus densiflora* forests. Vegetatio 122: 157–165.
- [7] Grime, J. (1987), Dominant and subordinate components of plant communities: implications for succession, stability and diversity. In: Gray, A. et al. (eds), Colonization, succession and stability: the 26th symposium of the British Ecological Society held jointly with the Linnean Society of London. pp. 413–428. Blackwell Scientific Publications, London.
- [8] Hong, S., Nakagoshi, N., & Kamada, M., (1995), Human impacts on pine-dominated vegetation in rural landscapes in Korea and western Japan. *Vegetatio* 116: 161–172.
- [9] Ito, S. (1977), Composition and Structure of plant community. 332pp. Asakura, Tokyo. (in Japanese)
- [10] Kamada, M. & Nakagoshi, N. (1991), The community structure and the dynamics of secondary vegetation in a rural area of middle Hiroshima Prefecture, Japan. *Journal of Japanese Forestry Society* 73: 276–282 (in Japanese with English summary).
- [11] Knight, D. H. (1991), Pine forests: A comparative overview of ecosystem structure and function. In: Nakagoshi, N. & Golley, F. B. (eds), Coniferous forest ecology, from an international perspective. pp. 121-135. SPB Academic publishing, The Hague.
- [12] Mitsudera, M., Kamata, Y. & Nakane, K. (1984), Effect of fire on water and major nutrient budgets in forest ecosystem III. Rainfall interception by forest canopy. *Japanese Journal of Ecology* 34: 15–25.
- [13] Miyawaki, A., Okuda S., & Mochizuki, R. (1983), Handbook of Japanese Vegetation Science. 672pp. Shibundo, Tokyo.

- [14] Mueller-Dombois, D. & Ellenberg, H. (1974), Aims and methods of vegetation ecology. 363pp. Wiley, New York
- [15] Nagamatsu, D. & Miura O. (1997), Soil disturbance regime in relation to micro-scale landforms and its effects on vegetation structure in a hilly area in Japan. *Plant Ecology* 133: 191–200.
- [16] Nakagoshi, N., Chinen, T., Hori, N., & Nehira, K. (1984), Regeneration of vegetation in the burned pine forest in southern Hiroshima Prefecture, Japan VI. Effects of topographical factor. *Memoirs of Faculty of Integrated Arts and Science*, *Hiroshima University Series* IV, 9: 41–65 (in Japanese with English summary).
- [17] Nakagoshi, N., Nakane, K., Imaide, H., & Nehira K. (1981), Regeneration of vegetation in the burned pine forest in southern Hiroshima Prefecture, Japan I. Floristic composition, vegetation structure and biomass in the early stage of regeneration. *Memoirs of Faculty of Integrated Arts and Science, Hiroshima University Series* IV, 6: 69–113 (in Japanese).
- [18] Nakagoshi, N., and Nehira K. (1982), Regeneration of vegetation in the burned pine forest in southern Hiroshima Prefecture, Japan III. The control forests. *Bulletin of the Biological Society of Hiroshima University* 48: 7–16 (in Japanese with English summary).
- [19] Nakagoshi, N., Nehira, K., & Nakane, K. (1983a), Regeneration of vegetation in the burned pine forest in southern Hiroshima Prefecture, Japan IV. Buried viable seeds in the early stage of succession. *Memoirs of Faculty of Integrated Arts and Science, Hiroshima University Series* IV, 8: 87–110 (in Japanese with English summary).
- [20] Nakagoshi, N., Nehira, K. & Takahashi, F. (1987a), The role of fire in pine forests of Japan. In: Trabaud, L. (ed), *The role of fire in ecological systems*. pp. 91–119. SPB Academic Publishing, The Hague.
- [21] Nakagoshi, N., Takamatsu, S., & Nehira, K. (1983b), Post-fire vegetation at 21 years old stand in Otake, southwestern Japan. Bulletin of the Biological Society of Hiroshima University 49: 23–33 (in Japanese with English summary).
- [22] Nakagoshi, N. (1987b), Post-fire succession of a pine forest in East Setouchi, Japan. *Papers of plant ecology to the memory of Dr. Satoshi Nakanishi*, 383–392.
- [23] Nakagoshi, N. & Touyama, Y. (1995), Disturbances and recovery processes of a pine forest ecosystem in a fire regime. *Journal of International; Development and Cooperation* (Hiroshima University), 1(1), 43–59.
- [24] National Workshop on Wildland Fire Activity in Canada (1997), *Workshop report*. Science Branch Canadian Forest Service Natural Resources Canada, Ottawa.
- [25] Ohtsuka, T. (1999), Early stages of secondary succession on abandoned cropland in north-east Borneo Island. *Ecological Research* 14: 281–290.
- [26] Rim, Y.-D., Kang, H.-K. Kang & Nakagoshi, N. (1991), Community ecology of Pinus densiflora forests in Korea. In Nakagoshi, N & Golley, F. B. (eds), Coniferous forest ecology, from an international perspective. pp. 17–30. SPB Academic publishing, The Hague.