Nat. Hist. Res., Vol. 3 No. 2: 161–171, March 1995

Succession of Secondary Pine Forests after Pine Wilt Disease in San-yô district, Western Japan*

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Abstract The main objective of the present study was to clarify the relationship between types of pine forest (*Querco glaucae–Pinetum densiflorae*) and the successional sere after pine wilt disease. Methods of analysis included phytosociological treatment, reconstruction of forest structure before the disease and size-structure analysis. Five vegetation types of pine forest were recognized from their species composition: (1) *Cladonia rangiferina* type; (2) *Eurya japonica* type; (3) *Quercus glauca* type; (4) *Ardisia japonica* type; and (5) *Ardisia crenata* type. The severity of disturbance by pine wilt disease increased from early successional stages, such as the *Cladonia rangiferina* type, to late successional stages, such as the *Ardisia crenata* type. In the early successional stages, pine forest remained after pine wilt disease, whereas there was a change to oak (*Q. serrata* Thunb. ex Murray, *Q. variabilis* Blume and *Q. glauca* Thunb. ex Murray) forests in the late successional stages.

Key words: Vegetation type, succession, severity of disturbance, pine wilt disease, *Querco glaucae–Pinetum densiflorae*

In the northern coastal region of the Inland Sea of Japan (San-yô district), forests have been strongly disturbed by human activities over a long period. Natural forests are rare except around shrines (Itow, 1983) and most forests are secondary ones dominated by Japanese red pine (*Pinus densiflora* Sieb. et Zucc.). Pine trees in these forests have been used for timber, shrubs for fuel and litter for compost. Pines can regenerate at sites where there has been forest-cutting, or at sites where forest fires have occurred, because Japanese red pine is a typical sun tree.

Since the 1960s pine forests have been abandoned, because propane gas and chemical fertilizer have become used widely in Japan, instead of shrubs and litter. Since then, pine forests have gradually changed into broad-leaved forests as vegetational succession proceeds. In addition, the abandoned pine forests have changed drastically since the 1960s, because of heavy damage by pine wilt disease. Catastrophic withering of pine forests was caused by a nematode [*Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickel] vectored mainly by a beetle (*Monochamus alternatus* Hope) (Kiyohara and Tokushige, 1971; Morimoto and Iwasaki, 1972). The severity of pine wilt disease was greater in mixed forest than in pure forest (Takeshita *et al.*, 1975). Inoue (1986) reported that pine wilt disease had increased after about 1971 in Okayama Prefecture. Yokobori (1986) forecast an area where catastrophic withering of pine forests would occur.

There have been some investigations on the succession of forests influenced by pine wilt disease (Nomoto *et al.*, 1985; Toyohara *et al.*, 1986; Fujihara *et al.*, 1991, 1992; Da and Ohsawa, 1992). Nomoto *et al.* (1985) reported two types of vegetation change in pine forests after pine wilt disease: (1) regeneration of pine and (2) succession from pine forests to *Quercus glauca* forests. Fujihara *et al.* (1992) suggested that the successional sere after pine wilt disease seems to vary depending on the severity of disturbance and the vegetation type before the disease. However, little is known about the

* A dissertation submitted in partial fulfilment of the requirements for the degree of Doctor of Science of Hiroshima University.

variations in the successional sere after pine wilt disease and the causes of these variations.

Toyohara (1984) conducted a phytosociological study of the secondary forests dominated by Japanese red pine in the northern coastal region of the Inland Sea, and recognized three associations: 1) *Querco glaucae–Pinetum densiflorae*; 2) *Querco myrsinaefoliae–Pinetum densiflorae*; and 3) *Querco salicinae–Pinetum densiflorae*. Among them, pine forests belonging to the *Querco glaucae–Pinetum densiflorae* are the most heavily disturbed by pine wilt disease (Toyohara, 1987).

The aim of this study was to clarify the relationship between types of secondary pine forest (*Querco glaucae–Pinetum densiflorae*) and the successional sere after pine wilt disease in the northern coastal region of the Inland Sea (San-yô district), western Japan.

Study sites

The northern coastal region of the Inland Sea (San-yô district) is situated 34°00′–35°20′N and 132°00′–134°25′E, lying south of the Chûgoku mountains in western Japan (Fig. 1). Low mountains with gentle slopes mainly prevail, but the southern part facing the Inland Sea consists largely of lowlands. Acidic rocks such as granite and rhyolite are laid down over almost the entire area and sedimentary rocks of Palaeozoic formations are scattered locally. The mean annual temperature is 15.4°C in Hiroshima, and 15.2°C in Okayama; correspondingly annual precipitation is 1608 mm, and 1202 mm respectively (Japan Meteorological Agency, 1982).

The potential vegetation of this area is considered to be evergreen broad-leaved forest (Nakanishi and Hattori, 1979) belonging to the Camellietea japonicae. At present, however, such natural forests are mostly destroyed and have been replaced by substitutional communities (Itow, 1983; Toyohara, 1984), such as secondary pine forest (*Querco glaucae–Pinetum densiflorae*).

Field surveys were carried out at three sites in this area (Fig. 1). Forest stands were chosen from representative sites disturbed by pine wilt disease in the 1970s (Ichinose) and the 1980s (Funakoshi). For comparison with these stands, one stand with no apparent pine wilt disease was also sampled (Ohno). The parent rock of all study sites is granite.

Methods

1. Field Surveys

The field surveys were carried out in 1986 and 1987. Four quadrats were established in

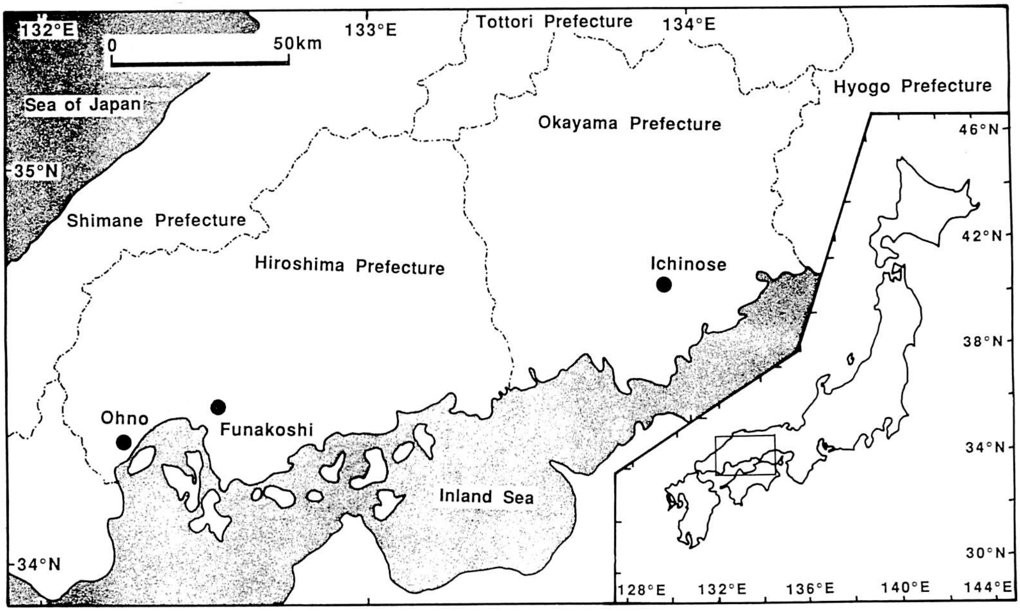

Fig. 1. Location of the study sites.

Ichinose, fifteen in Funakoshi and five in Ohno. Most quadrats were located on south-facing slopes at elevations between 35 m and 200 m. The quadrat size ranged from 52.5 m^2 to 216 m^2.

Cover-abundance and sociability (Braun-Blanquet, 1964) of all vascular plants and lichens were recorded in each quadrat. In addition, species name, tree height (H), trunk diameter at a height equal to 1/10 of tree height ($D_{0.1}$) were recorded for living trees and standing dead pine trees taller than 1 m. Trunk diameter at ground level (D_0) was also recorded for fallen dead pines in Funakoshi and in Ichinose. Because the stumps of most Japanese red pines killed by pine wilt usually remain for some decades, these stumps can be used as good indicators of the past prevalence of pine wilt disease. There were no dead pines in Ohno in 1987, where no apparent pine wilt has been recorded.

The names of species followed Ohwi and Kitagawa (1983) for flowering plants, Ohwi and Nakaike (1978) for ferns and Yoshimura (1974) for lichens.

2. Classification of Sample Stands

Classification of communities was made on the basis of species fidelity, species combination and physiognomy (Braun-Blanquet, 1964; Mueller-Dombois and Ellenberg, 1974). These data were analyzed by the computer program, Veget (Hada and Toyohara, 1990).

3. Reconstruction of Stand Structure before Disease

To reconstruct the structure of forests before disease, fallen dead pine trees were analyzed by the following procedures.

Trunk diameter at a height equal to 1/10 of tree height ($D_{0.1}$) for fallen dead pine trees was estimated from the diameter of the remaining trunk at ground level (D_0) using the following equation (Fujihara *et al.*, 1992):

$$D_{0.1} = 0.88 \times D_0 + 0.22$$

Nishioka *et al.* (1979) simplified a hyperbolic equation relating the diameter of the trunk at breast height (DBH) to the height (H) of trees [$1/H = 1/(A \times \mathrm{DBH}^h) + 1/H^*$] (Ogawa *et al.*, 1965) to the equation [$1/H = 1/(A \times \mathrm{DBH}) + 1/H^*$] in the case of pine forests. In the present study, the height (H) of fallen dead pine trees was estimated from trunk diameter at a height equal to 1/10 of tree height ($D_{0.1}$) by using the following equation.

$$1/H = 1/(A \times D_{0.1}) + 1/H^*$$

where A and H^* are coefficients specific to forests, and were calculated from standing trees in each quadrat by the least squares method. In quadrats I-3 and I-4 (Ichinose), tall trees disappeared in the 1970s. In order to estimate the height of dead pine trees, coefficients (A and H^*) were derived from the data obtained at stands in Ohno, which belonged to the same vegetation type.

4. Severity of disturbance

In Funakoshi most of the dead pine trees remained standing when the field survey was carried out. Because the remaining pine trees did not grow so much, the severity of disturbance (%) was expressed as a percentage of the basal area of dead pine trees at ground level to the total basal area of living and dead pine trees at ground level in each quadrat.

Results

1. Types of Secondary Pine Forest

Five types of secondary pine forest were recognized (Table 1). All stands belonged to the *Querco glaucae–Pinetum densiflorae* and were characterized by sun trees such as *Rhododendron reticulatum*, *Lyonia ovalifolia* var. *elliptica* and *R. kaempferi*. Among five vegetation types, *Cladonia rangiferina* type, which is found in Ohno, is characterized by the occurrence of lichen, such as *Cladia aggregata*. *Eurya japonica* type is characterized by the occurrence of shrubs, such as *E. japonica*, and dominated by *Dicranopteris linearis* in the herb layer. *Quercus glauca* type is characterized by the occurrence of evergreen broad-leaved trees, such as *Q. glauca*, *Symplocos lucida*, *Ligustrum japonicum* etc. *Ardisia japonica* type is characterized by the occurrence of *A. japonica*, *Dendropanax trifidus* and *Ilex chinensis* in addition to the characteristic species of the *Quercus glauca* type. *Ardisia crenata* type is characterized by

Table 1. Species composition of secondary pine forest.

Vegetation type 1)	*Cladinia rangiferina* type	*Eurya japonica* type							*Quercus glauca* type					*Ardisia japonica* type				*Ardisia crenata* type						
Quadrat number	O-1	O-2	F-1	F-14	F-2	F-10	F-13	I-1	O-3	F-7	F-15	F-9	I-2	O-4	F-3	F-11	I-3	O-5	F-12	F-6	F-4	F-8	F-5	I-4
Number of species	20	19	16	24	18	15	13	27	20	19	23	14	26	27	24	20	35	38	30	33	30	41	27	31
1.Miscanthus sinensis group																								
Miscanthus sinensis	+.2 2)	+	+	+	.	+	+	+	+	+.2	+	+	1.1	+	+	.	+	+	.	.	+	.	.	.
Juniperus rigida	1.1	1.1	+	+	+.2	+	1.1	+	+	1.1	+	+	1.1	+	+	.	+	.	+	.	+	+	.	+
Vaccinium oldhamii	+	+	.	+	+	.	.	+.2	+	1.1	+	.	1.1	.	.	.	1.1	.	.	+	+	+	.	1.1
Amelanchier asiatica	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+.2
Pteridium aquilium var. *latiusculum*	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.
2.Pinus densiflora group																								
Pinus densiflora	4.4	3.3	5.5	2.2	4.4	3.3	3.3	3.3	3.3	4.4	4.4	4.4	3.3	5.5	4.4	4.4	1.1	5.5	4.4	5.5	4.4	4.4	4.4	1.1
3.Rhododendron reticulatum group																								
Rhododendron reticulatum	+	2.2	.	1.1	2.2	.	+	3.3	+.2	2.2	3.3	1.1	2.2	3.3	1.1	.	2.2	.	2.2	+.2	.	+	+	1.1
Lyonia ovalifolia	1.2	1.1	1.1	1.1	1.1	1.1	1.1	2.2	1.1	3.3	2.2	3.3	1.1	1.1	3.3	3.3	+	1.1	3.3	1.2	3.3	3.3	3.3	+
Rhododendron kaempferi	1.2	1.1	+	+	+.2	+.2	+	+	+	+.2	.	.	+	.	+	.	2.2	1.1	+	.	.	+	.	+
Quercus serrata	+	+	1.1	+.2	+	+	.	+	.	+	.	.	+	.	.	.	3.3	.	+	+	.	.	.	1.1
4.Cladonia rangiferina group																								
Cladia aggregata	2.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5.Eurya japonica group																								
Eurya japonica	2.2	2.2	1.1	+	2.2	1.1	1.1	+.2	3.3	2.2	3.3	3.3	2.2	3.3	3.3	4.4	2.3	3.3	3.3	2.2	3.3	3.3	3.3	+
6.Quercus glauca group																								
Quercus glauca	.	.	.	.	.	.	.	.	+	+	+	+	.	+	+	+	.	+	+	+	+.2	+	+	1.1
Symplocos lucida	.	.	.	.	.	.	.	.	.	+.2	+	+	.	.	1.1	+	.	+	.	1.1	+	+	1.1	.
Ligustrum japonicum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	+	+.2	+	+	+.2	+	.
Neolistea sericea	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	1.1	.	.	+	+	+	.	+	.
Rhus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1.1	+	+	1.1	.	.
Photinia glabra	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	+	.	.	+.2
Cinnamomum japonicum	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Camellia japonica	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.
7.Ardisia japonica group																								
Ardisia japonica	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	+	.	+	.	+.2
Dedropanax trifidus	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	+	1.1	+.2	+	.
Ilex chinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	1.1	+	+	.	.	+	.	.
8.Ardisia crenata group																								
Ardisia crenata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+.2	
Dryopteris erythrosora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	+	+
Hedera rhombea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	+	+	.	.
Trachelospermum asiaticum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.
9.Pieris japonica group																								
Pieris japonica	.	.	.	.	.	.	.	.	1.1	.	.	.	+	.	+	.	.	+	.	1.2	.	.	.	.
Vaccinium smalii var. *glabrum*	.	+	.	.	.	.	.	.	+	.	+	.	.	+.2	+	+	.	.	+.2	.	+	+	+	.
Rhamnus crenata	.	.	+	+	+	+	.	.	.	+	.	+	.	1.1	.	.	.	+	.	1.1	.	.	.	.
Ilex pedunculosa	+	.	.	.	+	.	+	1.1	.	.	.	.	1.1	+	.	.	+	+	.	.	.	.	.	+
Ilex crenata	.	+	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Clethra barbinervis	.	.	.	+	.	.	.	.	.	.	1.1	.	.	.	.	.	.	.	.	.	.	1.1	.	.

the occurrence of shade-torelant species, such as *A. crenata*, *Dryopteris erythrosora*, *Hedera rhombea* and *Trachelospermum asiaticum* in addition to the characteristic species of the *Quercus glauca* type and the *Ardisia japonica* type. The number of species, especially the component of evergreen broad-leaved forests, increases from the *Cladonia rangiferina* and *Eurya japonica* types to the *Ardisia crenata* type.

2. Severity of Disturbance of Pine Forests by Pine Wilt Disease

In the *Eurya japonica* type, disturbance was less heavy (mean 23.9%), whereas disturbance was quite heavy in the *Quercus glauca* (55.7%), *Ardisia japonica* (64.6%) and *Ardisia crenata* types (87.3%) in Funakoshi (Table 2). The *Cladonia rangiferina* type was not found in Funakoshi.

3. Volume of Trees

Table 3 shows the volume ($D_{0.1}{}^2H$) of trees in each vegetation type. In Ohno, the total volume of the stand increased from the *Cladonia rangiferina* and *Eurya japonica* types to the *Ardisia crenata* type. *Pinus densiflora* dominated in all stands. *Quercus glauca* existed in the *Ardisia crenata* type, but its volume was

Table 1. (continued)

Vegetation type	*Cladinia rangiferina* type	*Eurya japonica* type							*Quercus glauca* type					*Ardisia japonica* type				*Ardisia crenata* type						
Quadrat number	O-1	O-2	F-1	F-14	F-2	F-10	F-13	I-1	O-3	F-7	F-15	F-9	I-2	O-4	F-3	F-11	I-3	O-5	F-12	F-6	F-4	F-8	F-5	I-4
10.Others																								
Rhus trichocarpa	+	1.1	+	+	+	1.1	+	1.1	+	1.1	1.1	1.1	2.2	+	1.1	+.2	1.1	+	+.2	1.2	2.2	1.1	1.1	2.2
Vaccinium bracteatum	2.2	1.1	2.2	+	2.2	+.2	+	+.2	2.2	2.2	.	+	+	1.1	1.1	+	+	1.1	+	+	1.1	+	+.2	+
Smilax china	+.2	+	+	+	+	+	.	+	+	+.2	+.2	+	+	2.2	+	+	2.2	+	+	+	+.2	+	+	+
Dicranopteris linearis	3.3	5.5	5.5	3.3	5.5	5.5	5.5	2.2	2.2	3.3	1.2	5.5	5.5	4.4	5.5	+	.	1.1	2.2	+	5.5	+.2	.	.
Viburnum wrightii	.	+	+	+	+	+	.	+	+	1.1	+	1.1	.	.	1.1	+	.	+	1.1	2.2	+	+	1.1	+
Paederia scandens	.	+	.	.	.	.	+	.	+	+	.	.	.	+	.	+	.	1.1	+	+	+	+	1.1	.
Akebia trifoliata	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	+	+	.	.	+	+	+	+
Cymbidium goeringii	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	+	+	+	+	1.1
Lespedeza bicolor	.	.	+	+	+	+	+	.	.	+.2	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Prunus jamasakura	.	.	.	+	+	.	.	+	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	+
Pourthiaea villosa var. *laevis*	+	+	.	+	.	.	.	.	.	.	.	.	.	+.2	.	+	+	.	.	.	.	.	.	.
Viburnum erosum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	.	+	+	.	+.2
Wikstroemia sikokiana	+.2	2.2	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.
Quercus variabilis	.	.	+	.	.	.	.	.	.	.	.	.	+	.	+	.	2.2	.	.	.	.	.	.	2.2
Alnus sieboldiana	.	.	.	+.2	.	.	.	.	.	.	.	.	.	2.2	.	.	.	1.1	.	+	.	1.2	.	.
Lindera umbellata	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	+	.	+	.	.
Styrax japonica	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.	.	.	.
Pleioblastus shibuyanus var. *viridis*	.	.	.	.	.	.	.	+.2	.	.	.	.	+	.	.	.	1.1	.	.	.	.	.	.	2.2
Sorbus alnifolia	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	1.1
Ampelopsis brevipedunculata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+	.	.
Oplismenus undulatifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	+	+	.
Acanthopanax sciadophilloides	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.
Carex floribunda	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
Carex conica	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1.1	.	.	.	.	.	.	+
Prunus verecunda	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	.	.	.	.
Viola grypoceras var. *exilis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	+	.	.
Mallotus japonicus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.
Wisteria floribunda	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1.1	.	.	+	.
Calamagrostis arundinacea var. *brachytricha*	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Rhus succedanea	.	.	.	.	+.2	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Sorbus japonica	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Lespedeza cyrtobotrya	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Pleioblastus chino var. *virdis*	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	+	.	.
Gardenia jasminoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+
Rhododendron macrosepalum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.1	.	.	.	.	.	.	1.1
Lindera glauca var. *laevis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+
Zanthoxylum schinifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.
Blechnum niponicum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.
Diospyros kaki	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.

Other species: Quadrat O-1: *Platycodon grandiflorum* +. Quadrat F-14: *Castanea crenata* +, *Arundinella hirta* +. Quadrat I-1: *Tripterospermum japonicum* +, *Aster scaber* +. Quadrat F-15: *Fraxinus sieboldiana* +, *Prunus grayana* 1.1, *Abelia spathulata* +, *Platanthera minor* +, *Gleichenia japonica* +. Quadrat I-2: *Andropogon virginicus* +, *Carex lenta* var. *lenta* +, *Rosa wichuraiana* +. Quadrat O-4: *Cryptomeria japonica* +, *Illicium religiosum* +. Quadrat I-3: *Solidago virga-aurea* var. *asiatica* +, *Lepisorus thunbergianus* +, *Lonicera japonica* +, *Pertya scandes* 1.1. Quadrat O-5: *Ficus erecta* +, *Parthenocissus tricuspidata* +, *Dryopteris varia* var. *setosa* +, *Ilex integra* +, *Aralia elata* +, *Tylophora aristolochioides* +, *Viola grypoceras* +. Quadrat F-4: *Evodiopanax innovans* +. Quadrat F-8: *Cleyera japonica* +.2, *Persea thunbergii* +, *Rhus ambigua* +, *Dioscorea japonica* +, *Smilax riparia* var. *ussuriensis* +, *Kadsura japonica* +, *Robina pseudo-acacia* +. Quadrat F-5: *Cinnamomum camphora* +, *Ophiopogon japonicus* +, *Aucuba japonica* +. Quadrat I-4: *Wisteria brachybotrys* +

1) All vegetation types belong to Querco glaucae-Pinetum densiflorae.

2) Cover-abandance and sociability (Braun-Blanquet 1964).

quite small.

In Funakoshi, the total volume of stands (volume of all dead and living trees) increased from the *Eurya japonica* type to *Ardisia crenata* type, as with the undisturbed forests in Ohno. However in Funakoshi the volume of living pine trees decreased in the *Ardisia crenata* and *A. japonica* types, because many pine trees were killed. In these types, evergreen broad-leaved tree such as *Quercus glauca* appeared, although their volumes were limited. On the other hand, pine trees still dominated in all

Table 2. Severity of disturbance in each vegetation type in the area disturbed in the 1980s.

Vegetation type	Severity of disturbance (%) [1)]
Eurya japonica type	0.0 - 43.3
Quercus glauca type	27.6 - 74.7
Ardisia japonica type	72.6 - 93.8
Ardisia crenata type	75.0 - 100.0

1) Severity of disturbance = (Basal area of dead pine trees / Basal area of dead and living pine trees) x 100

quadrats of the *Eurya japonica* type.

In Ichinose the volume of dead pine trees was large in the *Ardisia japonica* and *A. crenata* types, whereas it was small in the *Eurya japonica* type. In the *Ardisia japonica* and *A. crenata* types, the total volume was less than in the *Quercus glauca* type, because of the death of pine trees, and *Q. variabilis* shared the largest portion of the total volume. In these types, another deciduous oak, *Q. serrata* also occurred and the evergreen broad-leaved oak, *Q. glauca* were seen in the shrub layer.

4. Height Frequency of Trees

Figure 2 shows the number of living trees in height classes at 2-m intervals for each vegetation type. In Ohno, pine trees existed in all height classes in the *Cladonia rangiferina* type (O-1), *Eurya japonica* type (O-2), and *Quercus glauca* type (O-3), whereas they were restricted to height classes taller than 6 m in the *Ardisia japonica* type (O-4), and *A. crenata* type (O-5). In the *A. crenata* type, evergreen broad-leaved trees such as *Quercus glauca*, *Symplocos lucida*, *Ilex chinensis* and *Dendropanax trifidus* were found in height classes lower than 4 m (Fig. 2-A).

In Funakoshi, pine trees existed in all height classes in the *Eurya japonica* type, whereas they were restricted to height classes taller than 4 m in the *Ardisia japonica* and *A. crenata* types, as in Ohno. In the *Quercus glauca* (F-9), *Ardisia japonica* (F-11) and *A. crenata* types (F-6), many canopy pines were dead, whereas in the *Eurya japonica* type (F-2), many pines were still alive (Fig. 2-B). In the *Quercus glauca* type, *Symplocos lucida* occurred in the shrub layer. In the *Ardisia japonica* and *A. crenata* types evergreen broad-leaved trees such as *Quercus glauca*, *Symplocos lucida* and *Dendropanax trifidus* existed in the shrub layer. The number of evergreen broad-leaved trees increased from

Table 3. Volume ($D_{0.1}{}^2H$) of dead pine and living trees of the main species.

Study site	Vegetation type	Quadrat	$D_{0.1}{}^2H$ (x100 $cm^2 \cdot m/100m^2$)							
			Dead pine trees	Living trees: *Pinus densiflora*	*Quercus serrata*	*Quercus variabilis*	*Quercus glauca*	Others	Total	Total
Undisturbed forests (Ohno)	*Cladonia rangiferina* type	O-1	-	14.0	*	0.0	0.0	1.3	15.3	-
	Eurya japonica type	O-2	-	6.8	0.0	0.0	0.0	2.5	9.3	-
	Quercus glauca type	O-3	-	67.6	0.0	0.0	0.0	4.5	72.1	-
	Ardisia japonica type	O-4	-	88.4	0.0	0.0	0.0	13.6	102.1	-
	Ardisia crenata type	O-5	-	121.3	0.0	0.0	*	5.1	126.5	-
Disturbed in the 1980s (Funakoshi)	*Eurya japonica* type	F-1	11.0	15.1	*	0.0	0.0	0.6	15.7	26.7
		F-14	0.0	12.6	0.0	0.0	0.0	0.3	13.0	13.0
		F-2	9.2	19.5	*	0.0	0.0	1.8	21.3	30.4
		F-10	7.2	8.9	*	0.0	0.0	0.7	9.6	16.8
		F-13	0.0	16.7	0.0	0.0	0.0	1.2	17.9	17.9
	Quercus glauca type	F-7	23.7	36.8	*	0.0	0.0	2.7	39.6	63.3
		F-15	17.8	50.1	0.0	0.0	0.0	6.7	56.7	74.6
		F-9	23.2	7.7	0.0	0.0	0.0	6.2	13.9	37.1
	Ardisia japonica type	F-3	36.0	14.5	0.0	0.0	*	8.2	22.7	58.7
		F-11	79.6	3.3	0.0	0.0	*	6.2	9.5	89.1
	Ardisia crenata type	F-12	78.0	24.0	1.7	0.0	0.0	4.4	30.2	108.2
		F-6	64.1	27.8	1.2	0.0	*	9.3	38.4	102.4
		F-4	113.4	0.0	0.0	0.0	*	4.9	4.9	118.3
		F-8	10.2	9.9	0.0	0.0	0.1	17.2	27.2	129.1
		F-5	153.2	0.0	0.0	0.0	0.0	10.3	10.3	163.4
Disturbed in the 1970s (Ichinose)	*Eurya japonica* type	I-1	17.3	23.2	0.0	0.0	0.0	4.2	27.4	-
	Quercus glauca type	I-2	11.9	22.9	*	0.0	0.0	3.8	26.7	-
	Ardisia japonica type	I-3	90.3	3.9	0.6	4.0	0.0	3.8	12.4	-
	Ardisia crenata type	I-4	51.0	1.3	0.1	6.8	0.8	1.6	10.4	-

* Asterisk means the value lower than 0.1

the *Eurya japonica* type to *Ardisia crenata* type.

In Ichinose, many pine trees were found in the *Eurya japonica* type (I-1) and *Quercus glauca* type (I-2) (Fig. 2-C). In the *Ardisia japonica* type (I-3), pine trees were few, and trees of *Quercus variabilis* lower than 10 m in height were found. In the *Ardisia crenata* type (I-4), pine trees were few. In the *Ardisia crenata* type, a deciduous oak, *Quercus variabilis*, dominated in height classes exceeding 6 m, whereas trees of *Q. glauca* less than 4 m in height were abundant.

Discussion

The severity of disturbance by pine wilt disease was heavy in the *Ardisia japonica* and *A. crenata* types. After disturbances, forests of these types changed to *Q. variabilis* forests in this study or to *Quercus glauca* forests (Fujihara *et al.*, 1991). In these type forests, the death of canopy pine trees due to pine wilt disease resulted in the marked reduction of mean diameters, heights and total volume of living trees and many canopy gaps were formed. In these canopy gaps, saplings and seedlings of deciduous oak species, such as *Q. serrata* and *Q. variabilis*, and evergreen broad-leaved trees, such as *Quercus glauca*, *Symplocos lucida*, *Ilex chinensis* and *Dendropanax trifidus*, can grow upward. Succession of severely disturbed pine forests after pine wilt disease depends on the occurrence of saplings or seedlings of the above-mentioned species.

In contrast, the severity of disturbance by pine wilt disease was less heavy in the *Cladonia rangiferina* and *Eurya japonica* types. In these types, the reduction of diameters, heights and volumes of living trees was less than in the *A. japonica* and *A. crenata* types. Seedlings and saplings of deciduous or evergreen broad-leaved trees, which can reach the canopy layer, were absent in the understory before the disease, whereas many seedlings or saplings of pines were usually found. Therefore, in the *Cladonia rangiferina* and *Eurya japonica* type, pine forests were still maintained after the disease.

In the *Quercus glauca* type, the severity of disturbance was intermediate between that in the *Cladonia rangiferina* type and in the *Ardisia crenata* type. In the understory of this forest type there were seedlings or saplings of deciduous or evergreen oak. These pine forests have changed to *Quercus serrata* forests (Fujihara, unpublished).

The different courses of vegetation succession among different vegetation types also correspond to the topographical location of forest stands, because *Cladonia rangiferina* and *Eurya japonica* types are usually located on the upper parts of slopes, whereas *Ardisia japonica* and *A. crenata* types are usually located on the lower parts.

From the view point of vegetational succession, the order of vegetation types, from the *Cladonia rangiferina* type through the *Eurya japonica* type, *Quercus glauca* type and *Ardisia japonica* type to the *A. crenata* type, is considered to reflect the successional order of pine forests from earlier to later stages (Fujihara *et al.* 1989).

A schema of the successional sere after an outbreak of pine wilt disease is shown in Fig. 3. In pine forests at early successional stages, the disturbance by disease was not very heavy, and the pine forests were maintained. In contrast, in pine forests at late stages of succession, disturbance of the pine forest by disease was heavy, and dominance in volume and basal area shifted from pine to oak trees, such as *Q. serrata* and *Q. variabilis* (deciduous broad-leaved trees) or *Q. glauca* (an evergreen broad-leaved tree).

Acknowledgements

I express my sincere appreciation to Prof. Z. Iwatsuki, Hiroshima University (now Hattori Botanical Laboratory, Okazaki Branch), for valuable suggestions, hours of consultation and academic guidance during my study program.

I am also grateful to Dr. G. Toyohara, lecturer at Hiroshima University, and Dr. Y. Hada, Professor at Okayama University of Science, for their kind guidance and encouragement during the course of this study. Thanks are also extended to Dr. M. Hara, Dr. C. Yonebayashi and Dr. T. Nakamura of the Natural History Museum and Institute, Chiba, for comments on the manuscript and my colleagues at Hiroshima University for assistance in the field.

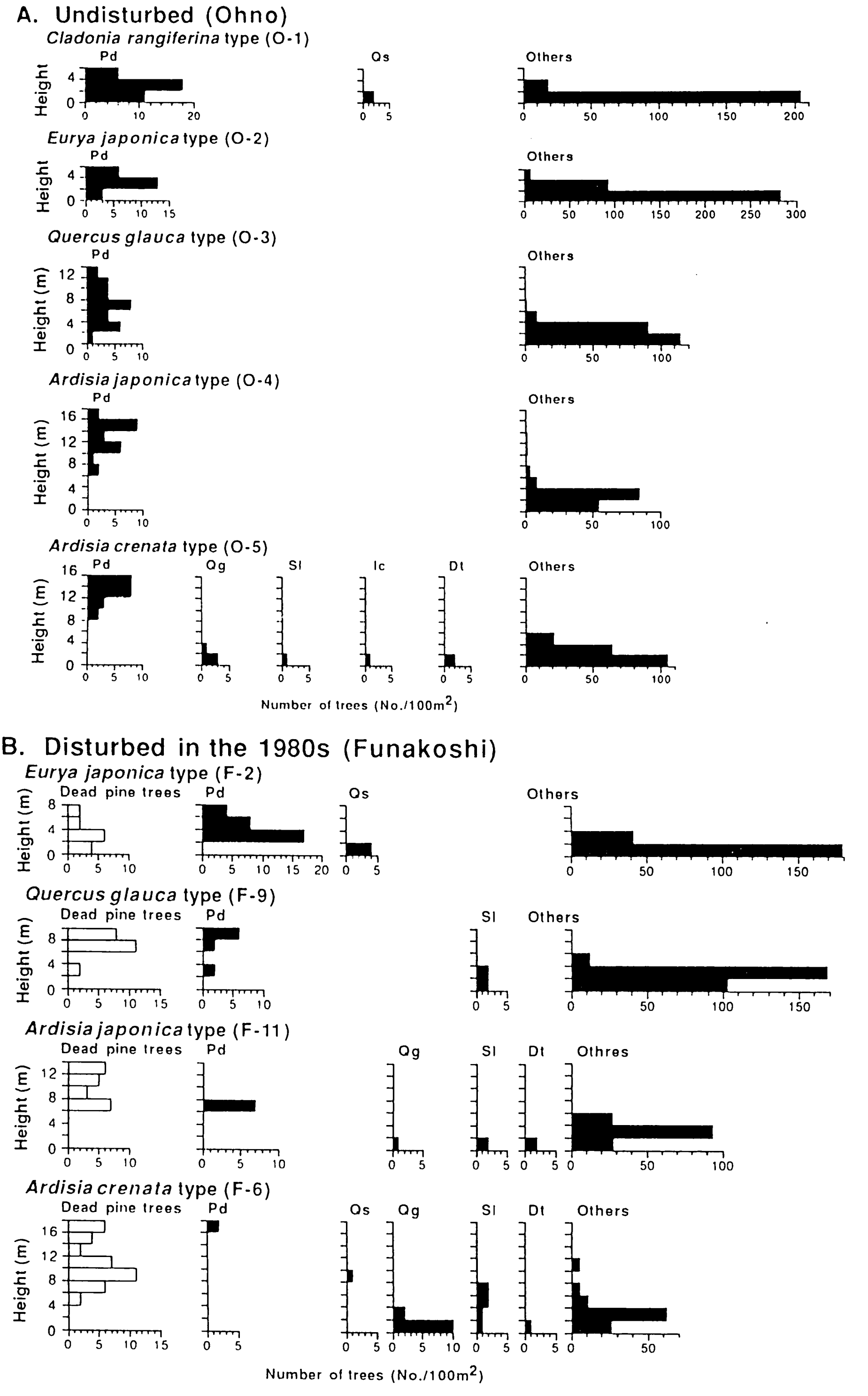
A. Undisturbed (Ohno)
Cladonia rangiferina type (O-1)
Eurya japonica type (O-2)
Quercus glauca type (O-3)
Ardisia japonica type (O-4)
Ardisia crenata type (O-5)
Pd
Qs
Qg
Sl
Ic
Dt
Others
Height
Height (m)
Number of trees (No./100m2)
B. Disturbed in the 1980s (Funakoshi)
Eurya japonica type (F-2)
Quercus glauca type (F-9)
Ardisia japonica type (F-11)
Ardisia crenata type (F-6)
Dead pine trees
Othres

Fig. 2

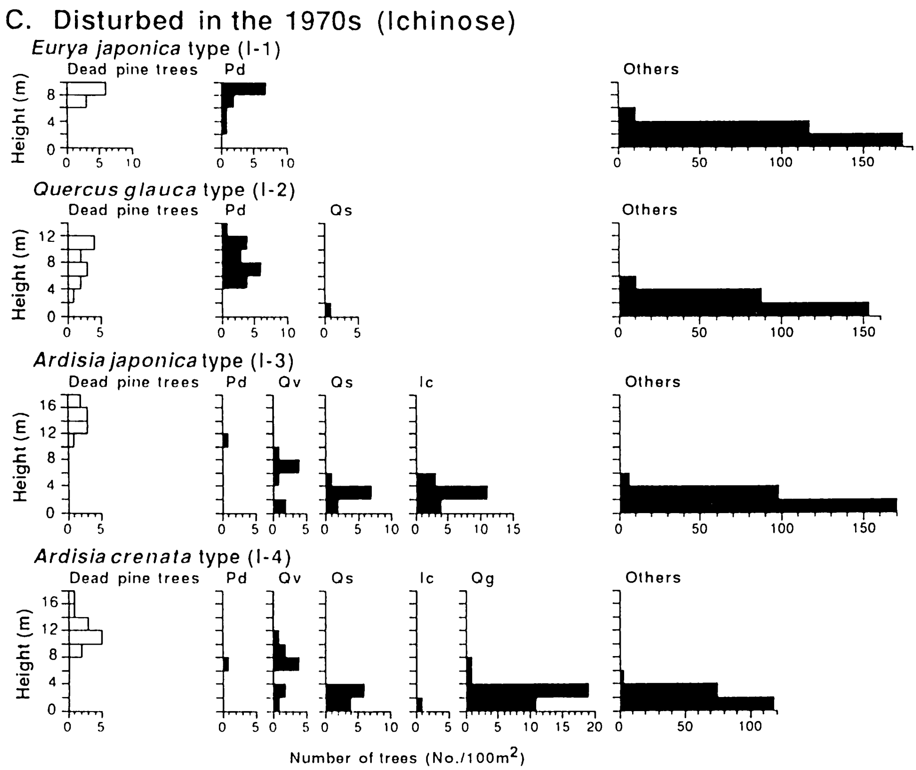

Fig. 2. Number of trees in height classes at 2-m intervals for dead pine (clear columns) and living trees (solid columns) in each vegetation type in the area undisturbed (A), disturbed in the 1980s (B) and disturbed in the 1970s (C). Pd: *Pinus densiflora*. Qs: *Quercus serrata*. Qv: *Q. variabilis*. Qg: *Q. glauca*. Sl: *Symplocos lucida*. Ic: *Ilex chinensis*. Dt: *Dendropanax trifidus*.

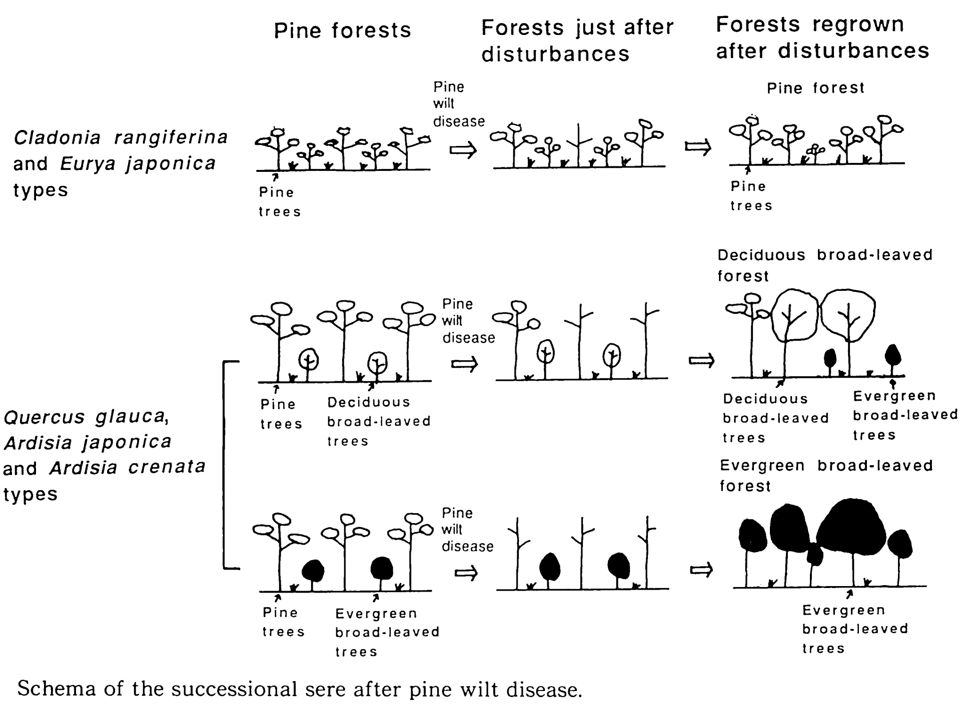

Fig. 3. Schema of the successional sere after pine wilt disease.

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(Accepted on 13 October 1994)

山陽地方におけるマツ枯れ後の遷移

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山陽地方沿岸部におけるマツ枯れ後の植生変化と植生単位との関係について明らかにした．種類組成からハナゴケ型，ヒサカキ型，アラカシ型，ヤブコウジ型およびマンリョウ型の５つの植生タイプが認められた．マツ枯れ被害度は，遷移初期のハナゴケ型から遷移後期のマンリョウ型になるにつれ増加した．遷移初期の植生タイプではマツ枯れ後もマツ林が維持されるのに対し，遷移後期の植生タイプでは，マツ枯れ後マツ林からコナラ林，アベマキ林およびアラカシ林へ変化することが明らかになった．

Appendix. Coefficients (A and H^*) and correlation coefficient (r) of the relationship $[1/H=1/(A\times D_{0.1})+1/H^*]$ between diameter of trunk at a height equal to 1/10 of tree height ($D_{0.1}$) and the height (H) of pine trees.

	Vegetation type	Quadrat	A	H*	r	Number of samples
Undisturbed forests (Ohno)	*Cladonia rangiferina* type	O-1	1.00	5.24	0.91	20
	Eurya japonica type	O-2	0.74	8.13	0.70	14
	Quercus glauca type	O-3	1.41	16.41	0.93	25
	Ardisia japonica type	O-4	1.68	27.53	0.88	29
	Ardisia crenata type	O-5	1.11	28.00	0.94	31
Disturbed in the 1980s (Funakoshi)	*Eurya japonica* type	F-1	1.20	5.59	0.49	15
		F-14	0.84	4.72	0.83	32
		F-2	0.51	13.51	0.75	18
		F-10	1.06	5.94	0.94	28
		F-13	1.37	4.94	0.69	25
	Quercus glauca type	F-7	0.88	20.21	0.82	20
		F-15	1.89	18.63	0.85	37
		F-9	1.91	10.77	0.78	19
	Ardisia japonica type	F-3	0.88	16.62	0.75	25
		F-11	1.80	16.63	0.86	20
	Ardisia crenata type	F-12	1.69	27.13	0.83	44
		F-6	2.18	28.89	0.96	21
		F-4	1.43	30.78	0.90	17
		F-8	2.82	20.22	0.57	31
		F-5	1.43	30.78	0.90	17
Disturbed in the 1970s (Ichinose)	*Eurya japonica* type	I-1	0.99	17.63	0.89	14
	Quercus glauca type	I-2	1.15	28.50	0.88	23
	Ardisia japonica type	I-3 1)	1.68	27.53	0.88	29
	Ardisia crenata type	I-4 2)	1.11	28.00	0.94	31

1) Coefficients are derived from the data of O-3 (*Ardisia japonica* type)

2) Coefficients are derived from the data of O-4 (*Ardisia crenata* type)