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Structure of *Pinus luchuensis* Forests Affected by Pine Wilt Disease in Northern Taiwan

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Abstract To clarify the succession of pine forests in northern Taiwan after pine wilt disease, the stand structure of *Pinus luchuensis* Mayr (Luchu pine) forests affected by the disease was described. Based on species composition, pine forests were classified into two types: 1) *Dicranopteris* type and 2) *Cyathea* type. The severity of disturbance judged by number of trees and by their basal area was, respectively, 62.8% and 80.2% in the *Dicranopteris* type and 67.5% and 61.6% in the *Cyathea* type. There was thus no clear difference in the severity of disturbance. The number of species in the *Cyathea* type was larger (50 and 75 species) than that in the *Dicranopteris* type (27 and 39 species). Evergreen broad-leaved trees, such as *Machilus thunbergii* Sieb. et Zucc., *M. zuihoensis* Hayata, *Schefflera octophylla* (Lour.) Harms and *Gordonia axillaris* (Roxb.) Dietr. were frequently present in the shrub layer, while trees belonging to Fagaceae, such as *Castanopsis* spp. were rare in both types. The disturbance by pine wilt disease also seems to accelerate the succession from pine to evergreen broad-leaved forest in Taiwan.

Key words: *Pinus luchuensis*, stand structure, succession, dominant species, *Dicranopteris* type, *Cyathea* type.

Pine forests are widely distributed in subtropical, temperate and the boreal region of East Asia. Pines are typical sun trees and require bare mineral soil for seed germination (Ahlgren and Ahlgren, 1981). They form the dominant forest on naturally or artificially disturbed areas. In Japan, secondary pine forests are composed of *Pinus densiflora* Sieb. et Zucc. (Japanese red pine), *P. thunbergii* Parl. (Japanese black pine) and *P. luchuensis* Mayr (Luchu pine). *P. densiflora* is distributed on Osumi Shoto, Kyushu Island, Shikoku Island, Honshu Island, and the southern part of Hokkaido Island, and *P. thunbergii* is distributed on Tokara Retto and northwards except for Hokkaido. The distribution of *P. luchuensis* is limited to the Ryukyu Islands, southern Japan (Tokara Retto, Amami Shoto, Okinawa Shoto and Sakishima Gunto), and is planted on the Bonin Islands.

The catastrophic withering of pine forests is caused by an epidemic nematode [*Bursaphelenchus xylophilus* (Steiner et Buhrer) Nickel], which is vectored by a beetle (*Monochamus alternatus* Hope) (Kiyohara and Tokushige, 1971; Morimoto and Iwasaki, 1972). Pine wilt disease has spread widely into most of Japan except its northernmost part, Hokkaido and Aomori Prefecture (Rutherford *et al.* 1990; Kishi, 1996).

Pinus luchuensis is as susceptible as *P. thunbergii* to pine wood nematode (Futai and Furuno, 1979; Kiyohara and Tokushige, 1971). *P. luchuensis* forests on Okinawa have been damaged by pine wilt disease since 1973 when affected pine trees were brought into the island from Kyushu for building materials, and the disease has expanded throughout the island (Ganeko, 1974; Kuniyoshi, 1974). In the Bonin Islands pine wilt disease has also been recorded (Enda, 1978). In the Taipei Prefecture of Taiwan wilted pines in a stand were observed in winter 1983 and the pine wood nematode was first identified from a *P. luchuensis* stand which had 50% mortality (Tzean and Jan, 1985; Mamiya, 1986). Enda (1988) also reported pine wilt disease in Taiwan.

Pine wilt disease drastically affects the dynamics of pine forests. In western Japan, disturbance by pine wilt disease leads to an acceleration of succession from Japanese red pine to oak forest (Fujihara, 1996). The succession of forests after pine wilt disease varies according to the species composition and structure of the pine forests before the disease, the severity of disturbance (Fujihara, 1995, 1996; Fujihara *et al.*, 1992), and the management of damaged pine forests after pine wilt disease (Sakamoto *et al.*, 1995; Toyohara *et al.*, 1986). Da and Ohsawa (1992) reported succession after mass die-back of pine forests and documented the deciduous broad-leaved tree species that were established after the die-back. The studies mentioned above were conducted in the areas severely disturbed by human activity and dominated by the secondary forests of Japanese red pine (*P. densiflora*) and deciduous oak (*Quercus* spp.). On coastal dunes of southern Kyushu, the succession of Japanese black pine (*P. thunbergii*) forest after pine wilt disease depends on the management of the forest floor (Taoda, 1988). Shimizu (1986, 1987, 1995) documented changes in species composition and structure of *P. luchuensis* forests after pine wood nematode infection on the Chichijima Islands. However, in the Ryukyu Islands and Taiwan, where deciduous oak forests are rare and evergreen broad-leaved forests dominate, little is known about the succession of *P. luchuensis* forests after pine wilt disease.

The main object of the present study was to describe the stand structure of damaged *Pinus luchuensis* forests and to clarify the succession of the pine forests after pine wilt disease in northern Taiwan.

Study Sites

The study area (25°25′N, 121°44′E, 350–360 m a.s.l.) is situated near Pinglin, about 20 km east of Taipei city, northern Taiwan (Fig. 1). The mean annual temperature at Pinglin is 19.6℃ and the annual precipitation is >2500 mm. According to the vegetation zonation on Taiwan by Su (1984), the area belongs to the *Castanopsis-Machilus* zone, where the natural vegetation is dominated by evergreen broad-leaved species such as *Castanopsis* spp., *Cyclobalanopsis* spp. and *Machilus* spp. However, some of natural evergreen broad-leaved forests have been converted to planted pine (*Pinus luchuensis*) forests and tea (*Camellia sinensis* (L.) O. Kuntze) gardens. The pine forests are distributed mainly along roadsides.

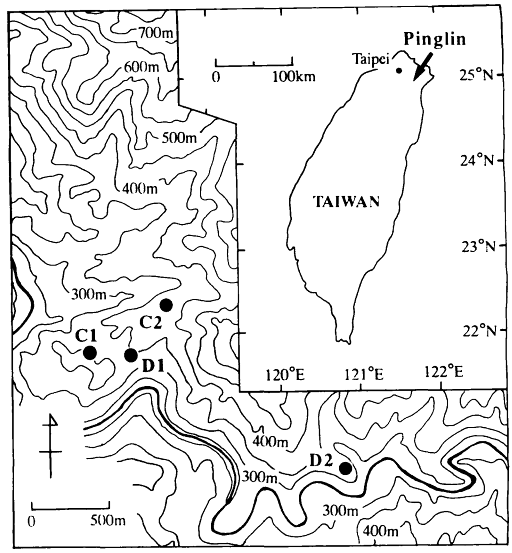

Fig. 1. Location map. C1, C2, D1 and D2 show locations of each quadrat.

Methods

Field survey was carried out in November, 1994. Quadrats (D1, D2, C1 and C2) of 10× 10 m were established in four pine forests. Cover-abundance and sociability (Braun-Blanquet, 1964) of all vascular plants were recorded in each quadrat. Trunk diameter at breast height (DBH) and tree height (H) were measured for trees taller than 1.2 m and their positions were mapped. Disks of trunks were collected from three trees (*Diospyros morrisiana* Hance and *Machilus zuihoensis* Hayata from C1 and *Mallotus paniculatus* var. *paniculatus* (Lamarck) Muell. Arg. from C2) at the ground level. Core sample of trunks were also obtained from pine trees (two to five trees in each quadrat) at 30 cm above ground level by using an increment borer.

The vegetation in each quadrat was classified based on the differences in species composition by the phytosociological method (Braun-Blanquet, 1964; Mueller-Dombois and Ellenberg, 1974). Two indices of the severity of disturbance by pine wilt disease were calculated based on relative number and relative basal area of dead pine trees to the total number and total basal area of living and dead pine trees in each quadrat.

The ring width of every year was measured for disks and cores by a binocularmicroscope. Ring widths of disks were measured along two perpendicular lines, one along the longest diameter through the pith and the other at right angles to this line. The mean of four ring widths for each year was calculated. If an increment core did not contain pith, the age of the tree was determined by the following procedure. The position of the pith was estimated from the curvature of the innermost ring, and the distance between the estimated pith and the innermost ring was measured. The width of each missing ring was expressed as the mean width of the five innermost rings. The number of missing rings was calculated by dividing the distance by the mean width of the five innermost rings. The sum of the number of rings and the number of estimated missing rings gives the age of the tree.

The nomenclature mainly follows Satake *et al.* (1982, 1989) and Flora of Taiwan, second edition (Editional Committee of Flora of Taiwan, Second Edition, 1993–1994).

Results

1. Vegetation types

The quadrats were classified into two types based on species composition; 1) *Dicranopteris* type and 2) *Cyathea* type (Table 1). The *Dicranopteris* type was characterized by the dominance of *Dicranopteris linearis* (Burm. fil.) Underw. in the understory and the occurrence of *Mallotus japonicus* (Thunb.) Muell. Arg. The *Cyathea* type was characterized by the abundant occurrence of *Cyathea* spp. (*C. lepifera* (J. Sm. ex Hook.) Copel. and *C. podophylla* (Hook.) Copel.) and comprised *Alpinia japonica* (Thunb.) Miq., *Maesa japonica* (Thunb.) Moritzi, *Oplismenus undulatifolius* (Arduino) Roemer et Schultes and *Ficus* spp. (*F. erecta* Thunb. var. *beecheyana* (Hook. et Arn.) King, *F. fistulosa* Reinw. ex Bl. and *F. formosana* Maxim.) in the herb and shrub layers. The *Dicranopteris* type was seen on a convex site which was probably relatively dry, whereas the *Cyathea* type was seen on a concave slope which was probably moist. Living trees of *Pinus luchuensis* still remained in all the quadrats investigated. Shade-intorelant species, such as *Clerodendrum cyrtophyllum* Turcz. and *Mallotus paniculatus* var. *paniculatus*, were found in all quadrats. *Alpinia intermedia* Gagnep., *Ardisia sieboldii* Miq., *Psychotria serpens* L. and *Wendlandia formosana* Cowan were also present in all quadrats. The number of species in the quadrat belonging to the *Cyathea* type was larger (50 and 75 species) than those belonging to the *Dicranopteris* type (27 and 39 species).

2. Severity of disturbance by pine wilt disease

Both indices of the severity of disturbance based on the relative number of dead trees and on the relative basal area were similar in the two vegetation types (Table 2), although the stem number and basal area of the pine trees were both larger in the *Dicranopteris* type than in the *Cyathea* type. The pine trees had probably died within the previous few years because they still standing with branches.

3. Distribution of trees

Figure 2 shows distribution maps for trees taller than 1.2 m in each quadrat: dead and living pine trees seem to exclude each other in quadrats D2, C1 and C2. In quadrat D2 a dense cover of *Dicranopteris linearis* seems to prevent seedlings from becoming established and growing. In the *Cyathea* type (C1 and C 2), *Cyathea lepifera* and *C. podophylla* seem to prevent seedling establishment because the leaves of *Cyathea* expand horizontally and occupy the forest floor and shrub layer.

4. Age and ring width of trees

Figure 3 shows the ring widths of sample trees in each quadrat. The age of pine trees ranges from 23 to 35 years old. The ring width was wider when the trees were young and became narrower with maturity, although it increased slightly in some trees around 1981. In D1, the age of the two pine trees were 27 and 28 years; in D2, two of the three trees were the same, 35 years old. However, in C1 (24–31 years) and C2 (23–30 years), the ranges were wider. The other species in C1 and C2 (*Machilus zuihoensis* and *Diospyros morrisiana* in C1, *Mallotus pa-*

Table 1. Cover-abundance and sociability of species which occurred in more than one quadrat (A) and in one quadrat (B).

(A)

Vegetation type	*Dicranopteris* type								*Cyathea* type							
Quadrat	D1				D2				C1				C2			
Layer*	T	ST	S	H	T	ST	S	H	T	ST	S	H	T	ST	S	H
Height (m)	12	7	5	0.6	16	9	5	0.8	14	9	5	0.6	15	9	5	0.6
Coverage (%)	40	20	40	95	20	10	20	80	60	30	40	60	60	5	30	30
No. of species	1	3	21	19	1	3	9	28	1	3	23	31	1	3	16	61
Total no. of species	39				27				50				75			
Alpinia intermedia				+				+			1.1	+				+
Ardisia sieboldii			+					+			+			1.2	1.2	+
Clerodendrum cyrtophyllum			+				+	+			+				+	+
Mallotus paniculatus var. *paniculatus*			+					+		+				+	+	
Pinus luchuensis	+	1.1			2.2	+			2.2				1.1			
Psychotria serpens			+					+				+				+
Wendlandia formosana			+					+		+	+				+	
Dicranopteris linearis				5.5				5.5				+.2				+
Mallotus japonicus		+		+		+										
Cyathea lepifera				+							2.2				+.2	+
Cyathea podophylla								1.1			1.1					3.3
Alpinia japonica												+				+
Ficus erecta var. *beecheyana*											+					+
Ficus fistulosa											+	+			+	
Ficus formosana											+	+				+
Maesa japonica											+	2.2			+	
Oplismenus undulatifolius												2.2				+
Melastoma candidum				+							+					+
Lasianthus fordii			+								+	+			2.2	+
Michelia compressa			+								+	+			1.2	+
Litsea rotundifolia							+					+			+	
Machilus zuihoensis							+				+	+			+	
Antidesma japonicum			+					+								+
Gordonia axillaris			+				1.1								+	
Machilus thunbergii				+		1.1	+									+
Smilax bracteata			+					+								
Diospyros morrisiana			+							+	+					
Miscanthus sinensis				+								+				
Smilax nervo-marginata				+								+				
Elaeocarpus japonicus			+												+	
Piper kadzura				+												+
Ampelopsis cantoniensis								+								+
Dioscorea pseudo-japonica								+								+
Zingiber kawagoii								+								+
Oplismenus compositus								+								+
Cyathea spinulosa								+								+
Glochidion acuminatum								+								+
Miscanthus floridulus								1.1								+
Paederia scandens								+								+
Schefflera octophylla							+								+.2	+

* T: Tree layer. ST: Subtree layer. S: Shrub layer. H: Herb layer.

Table 1. (continued)

(B)

D1	
Subtree layer	
Prunus phaeosticta	+
Shrub layer	
Pithccerobium lucidum	2.2
Randia cochinchinensis	1.1
Castanopsis carlesii var. *sessilis*	+
Euonymus sp.	+
Glochidion rubrum	+
Itea oldamii	+
Myrsine seguinii	+
Sapium discolor	+
Herb layer	
Castanopsis carlesii var. *sessilis*	+
Cocculus trilobus	+
Myrsine seguinii	+
Pithocerobium lucidum	+
Trachelospermum asiaticum	+

D2	
Subtree layer	
Fraxinus insularis	2.2
Shrub layer	
Adinandra formosana	+
Archidendron lucidum	+
Rhus sylvestris	+
Herb layer	
Anodendron affine	+
Cayratia tenuifolia	+
Daphniphyllum teijsmanii	+
Dioscorea cirrhosa	+
Elaeocarpus sylvestris	+
Rhus sylvestris	+
Sinomenium acutum	+
Smilax lanceifolia	+
Smilax sebeana	+
Cynanchum formosanum	+

C1	
Subtree layer	
Aleurites cordata	+
Shrub layer	
Ficus oxyphylla	+
Ardisia quinquegona	+
Eurya acuminata	+
Eurya japonica	+
Helicia cochinchinensis	+
Ilex maximowicziana	+
Symplocos glauca	+
Turpinia ternata	+
Herb layer	+
Cocculus orbiculatus	+
Glochidion triandrum	+
Selaginella longifolia?	+
Ficus oxyphylla	+
Smilax sp.	+
Meliosma rigida	+
Pothos chinensis	+
Psychotria rubra	+

C2	
Shrub layer	
Camellia sinensis	1.2
Saurauja oldhamii	+
Cleyera japonica	+
Lasianthus wallichii	+
Lindera communis	+
Herb layer	
Calanthe formosana	1.1
Camellia sinensis	+
Cyathea hancockii	+.2
Staurogyne concinnula	+.2
Nephrolepis auriwlata	+.2
Pronephrium simplex	+.2
Selaginella doederleinii	+.2
Alocasia odora	+
Angiopteris lygodiifolia	+
Blechnum orientale	+
Curculigo capitulata	+
Cymbidium lancifolium	+
Cyratia sp.	+
Desmodium laxum ssp. *leptopus*	+
Forvestia chinensis	+
Heterosmilax japonica	+
Hydrangea chinensis	+
Lasianthus curtisii	+
Lasianthus wallichii	+
Lemmaphyllum microphyllum	+
Lindera communis	+
Liparis nigra	+
Liparis sp.	+
Microsorium buergerianum	+
Microstegium vimineum var. *polystecium*	+
Morinda umbellata	+
Mussaenda parviflora	+
Percemphyllus formosanus	+
Pronephrium triphyllum	+
Rubus corchorifolius	+
Sarcandra glabra	+
Setaria palmifolia	+
Smilax china var. kuru	+
Tetrastigma formosanum	+
Urena lobata	+
Vernonia andersonii var. *albipappa*	+

niculatus var. *paniculatus* in C2) were younger than the pine trees, indicating that they had invaded after the pine trees had been planted.

5. Height frequencies of trees

As shown in Table 3 and Fig. 4, many of the canopy pine trees were already dead in all quadrats; however no other species reached the height of living pine trees, and the canopy was still composed of *Pinus luchuensis* only. The trunk densities in the lower classes were higher except for D2 where *Dicranopteris linearis* densely covered the forest floor. Shade-intorelant species, such as *Mallotus japonicus, M. paniculatus* var. *paniculatus* and *Clerodendrum crytophyllum* were frequently found in the understory. Large-tree species, which could become dominants of the canopy layer were rare in the understory, although there were many tree and subtree species, such as *Prunus phaeosticta*

Table 2. Number and basal area of living and dead pine trees and severity of pine tree disturbance.

Vegetation type	*Dicranopteris* type		*Cyathea* type	
Quadrat	D1	D2	C1	C2
Number of tree				
Live pine (No./100m^2)	7	3	3	2
Dead pine (No./100m^2)	6	10	4	7
Total (No./100m^2)	13	13	7	9
Severity of disturbance (%)*	46.2	76.9	57.1	77.8
Basal area				
Live pine (cm^2/100m^2)	715.6	920.7	1058.9	660.2
Dead pine (cm^2/100m^2)	2553.8	4324.0	1463.2	1369.0
Total (cm^2/100m^2)	3269.4	5244.7	2522.1	2029.2
Severity of disturbance (%)**	78.1	82.4	58.0	67.5

* (Number of dead pine trees / Number of dead and living pine trees) x 100
** (BA of dead pine trees / BA of dead and living pine trees) x 100

(Hance) Maxim., *Myrsine seguinii* Lév., *Diospyros morrisiana*, *Michelia compressa* (Maxim.) Sargent, *Gordonia axillaris* (Roxb.) Dietr., *Elaeocarpus japonicus* Sieb. et Zucc., *Ardisia sieboldii*, *Cleyera japonica* Thunb. and *Schefflera octophylla* (Lour.) Harms. These species usually form the subtree layer in natural evergreen broad-leaved forests. Shrub species such as *Antidesma japonicum* Sieb. et Zucc., *Randia cochinchinensis* (Lour.) Merr., *Glochidion rubrum* Blume etc. were also found in height classes lower than 4 m. Most species in the understory were evergreen except for some shade-intolerant ones.

6. Basal area of species

Except for quadrat C2, the basal area of living *Pinus luchuensis* was the largest in each quadrat (Table 4). Basal area of some of the evergreen broad-leaved species such as *Ardisia sieboldii*, *Prunus phaeosticta*, *Diospyros morrisiana*, *Machilus thunbergii*, *Wendlandia formosana* was larger than 100 cm^2/100 m^2 in each quadrat. Deciduous species occupied only a small portion of the basal area (3.1–15.4%) in every quadrat.

Figure 5 shows rank-abundance curves for each quadrat. The basal area of each species was plotted in the species order. *Pinus luchuensis* was dominant in three quadrats (D1, D2, C1). Many evergreen broad-leaved species, such as *Prunus phaeosticta* and *Diospyros morrisiana*, etc., which occur in the natural evergreen broad-leaved forests, were found in the middle part of curves. Therefore these species will become co-dominant after pine wilt

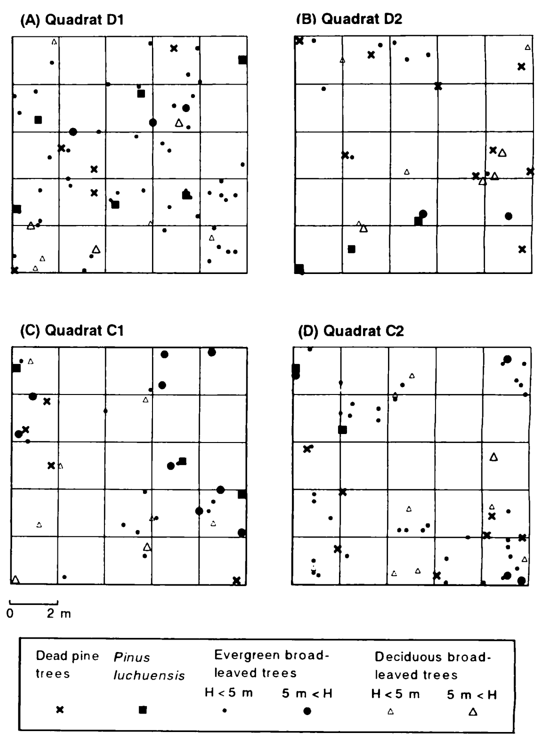

Fig. 2. Distribution of dead pine trees and living trees taller than 1.2 m in each quadrat. Top of each figure represents upper part of slope of each quadrat. H means tree height.

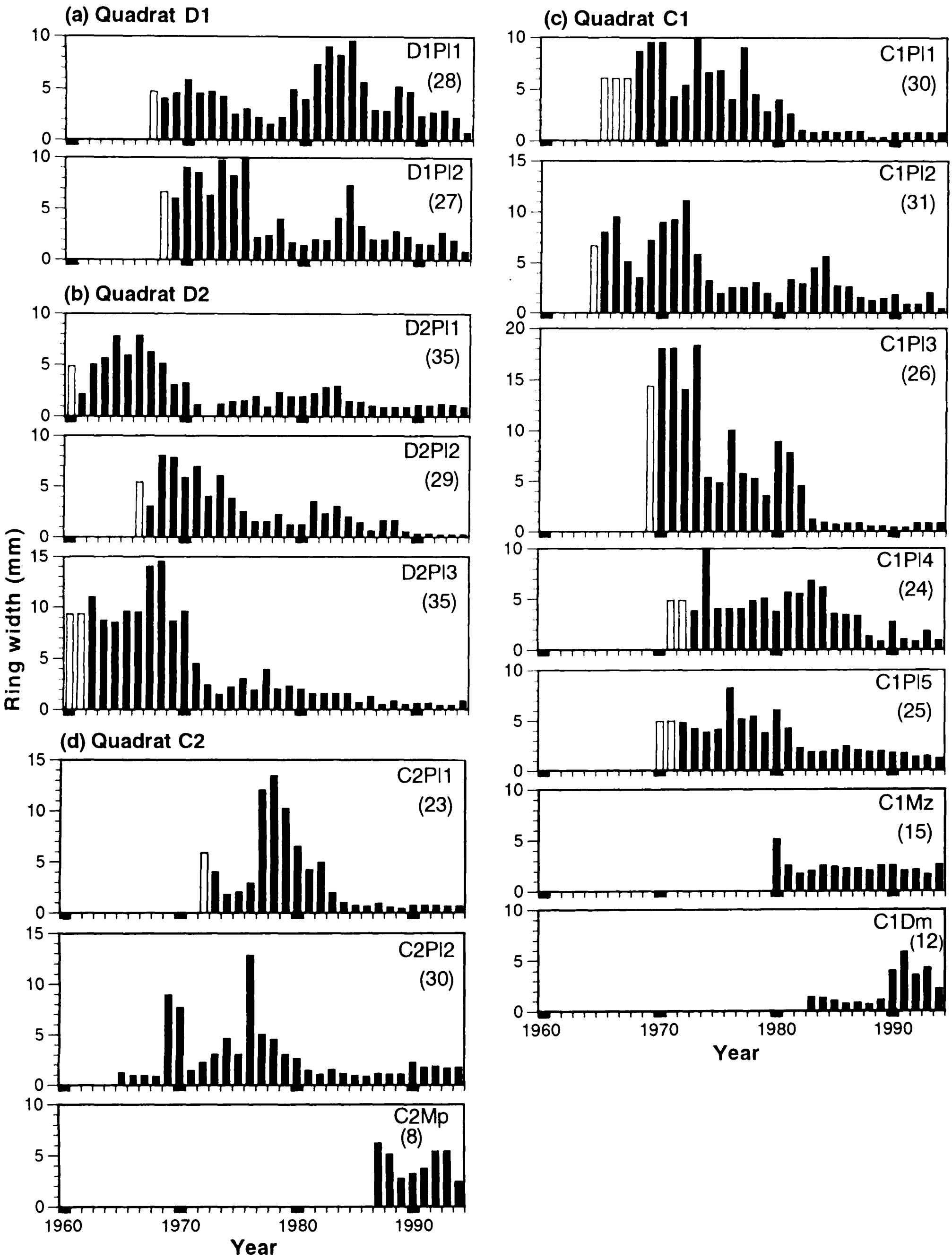

Fig. 3. Ring widths of sample trees from each quadrat. Pl: *Pinus luchuensis*. Mp: *Mallotus paniculatus* var. *paniculatus*. Mz: *Machilus zuihoensis*. Dm: *Diospyros morrisiana*. Open column indicates width of missing rings estimated. Sample number is shown on the right upper side of each figure. Number in parenthesis means age of tree. See text for methods.

disease.

Discussion

In Japan, pine forests have been widely used for a long time. Various types of pine forest belonging to different stages of succession can be recognized in relation to differences in human disturbance. On the other

Table 3. Frequency distributions of living trees and dead pine trees in height classes in each quadrat.

(a) Quadrat D1

Species	Height class (m)								
	1-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	Total
Living trees									
Pithocerobium lucidum	3	11							14
Gordonia axillaris	2	7							9
Randia cochinchinensis	2	6							8
Pinus luchuensis			3	1	1	1			6
Diospyros morrisiana	3		1						4
Michelia compressa	2	2							4
Mallotus japonicus			1	2					3
Wendlandia formosana		3							3
Clerodendrum cyrtophyllum	1	2							3
Antidesma japonicum	2	1							3
Itea oldhamii	2	1							3
Prunus phaeosticta			1	1					2
Myrsine seguinii	1		1						2
Glochidion rubrum		2							2
Castanopsis carlesii var. *sessilis*			1						1
Eounymus sp.			1						1
Sapium discolor			1						1
Ardisia sieboldii		1							1
Elaeocarpus japonicus		1							1
Lasianthus fordii	1								1
Mallotus paniculatus var. *paniculatus*	1								1
Subtotal	20	37	10	4	1	1	0	0	73
Dead pine	0	0	0	1	0	0	1	3	5
Total	20	37	10	5	1	1	1	3	78

(b) Quadrat D2

Species	Height class (m)								
	1-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	Total
Living trees									
Fraxinus insularis			4	2					6
Pinus luchuensis					1	1	0	1	3
Gordonia axillaris	1	2							3
Machilus thunbergii			2						2
Machilus zuihoensis		2							2
Adinandra formosana	1	1							2
Clerodendrum crytophyllum	2								2
Rhus sylvestris		1							1
Schefflera octophylla		1							1
Archidendron lucidum		1							1
Litsea lotundifolia		1							1
Mallotus japonicus		1							1
Subtotal	4	9	6	2	1	1	0	1	25
Dead pine	3	0	0	0	1	0	5	1	10
Total	7	9	6	2	2	1	5	2	32

Table 3. (continued)
(c) Quadrat C1

Species	Height class (m)							
	1-2	2-4	4-6	6-8	8-10	10-12	12-14	Total
Living trees								
Wendlandia formosana	1	4	8					13
Maesa japonica	10							10
Diospyros morrisiana		1	2	3				6
Machilus zuihoensis		1	3					4
Pinus luchuensis						1	2	3
Eurya acuminata		2						2
Ficus fistulosa		2						2
Clerodendrum crytophyllum	1	1						2
Ardisia sieboldii		2						2
Ficus formosana	2							2
Mallotus paniculatus var. *paniculatus*					1			1
Aleurites cordata			1					1
Eurya japonica		1						1
Michelia compressa			1					1
Helicia cochinchinensis		1						1
Turpinia ternata		1						1
Melastomata candidum		1						1
Symplocos glauca	1							1
Ficus erecta var. *beecheyana*	1							1
Subtotal	17	18	15	3	1	1	2	57
Dead pine	0	0	0	1	2	0	1	4
Total	17	18	15	4	3	1	3	61

(d) Quadrat C2

Species	Hight class (m)								
	1-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	Total
Living trees									
Ardisia sieboldii		3		1	3	1			8
Lasianthus fordii	8								8
Michelia compressa	3	3							6
Camellia sinensis	5								5
Machilus zuihoensis	1	2	1						4
Ficus fistulosa	1	3							4
Lasianthus wallichii	4								4
Pinus luchuensis							1	2	3
Mallotus paniclatus var. *paniculatus*		1	2						3
Schefflera octophylla		2	1						3
Cleyera japonica			2						2
Clerodendrum crytophyllum		2							2
Lindera communis		2							2
Wendlandia formosana	1	1							2
Maesa japonica	2								2
Elaeocarpus japonicus		1							1
Sauranja oldhamii	1								1
Gordonia axillaris	1								1
Subtotal	27	20	6	1	3	1	1	2	61
Dead pine	1	0	1	0	3	1	1	0	7
Total	28	20	7	1	6	2	2	2	68

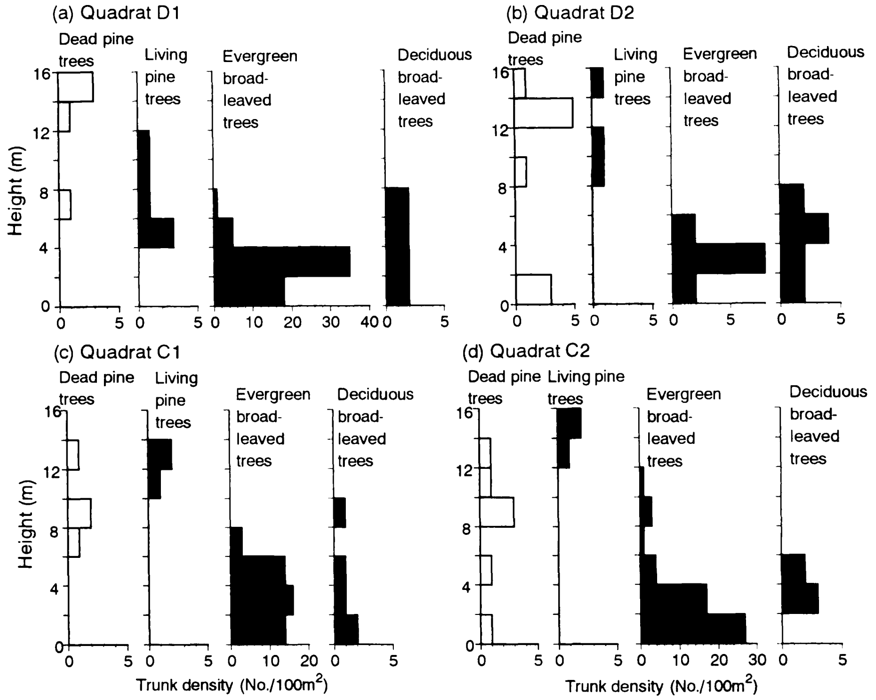

Fig. 4. Height frequencies of dead pine trees and living trees taller than 1.2 m in each quadrat.

hand, *Pinus luchuensis* is not indigenous to Taiwan and does not have a long history. Two vegetation types were recognized in the present study. These types appear to correspond to the difference in topography rather than in human disturbance. The largest difference between the two types lies in the species composition and coverage of the herb layer. The *Dicranopteris* type was established on the dry convex slope while the *Cyathea* type was established on the moist concave slope.

In western Japan, when pine forests at the earlier stages of succession are disturbed by pine wilt disease, the disturbance is not so severe, and some of the infected forests are maintained as pine forests. In contrast, when pine forests are disturbed by the disease at later stages of succession, the disturbance is severe and the dominant species shift from pine to oaks, such as *Quercus serrata* and *Q. variabilis* Blume (deciduous species) or *Q. glauca* Thunb. ex Murray (evergreen species) (Fujihara, 1995). In the present study, there was no clear difference in the severity of disturbance by pine wilt disease between the *Dicranopteris* and *Cyathea* types. It appears that the pine forests will not to be maintained after the pine wilt disease in either type and they will change into evergreen broad-leaved forests, because there are few open sites suitable for regeneration of pine trees. Many evergreen broad-leaved trees, such as *Machilus thunbergii*, *Schefflera octophylla* and *Prunus phaeosticta*, already exist in the understory of pine forests, although succession after pine wilt disease may sometimes be hindered by the dense cover of *Dicranopteris linearis*. Shade-intolerant deciduous shrubs and subtrees, such as *Mallotus japonicus*, *M. paniculatus* var. *paniculatus* and *Clerodendrum cyrtophyllum* are seen in the earlier stage of succession, but are gradually replaced by shade-tolerant evergreen broad-leaved trees.

The species composition of the regrown evergreen broad-leaved forests does, however, appear to differ from that of natural evergreen broad-leaved forest, the main components of which are Fagaceae. The absence of Fagaceae in the damaged pine forests means that the establishment of seedlings of Fagaceae such as *Castanopsis*, are delayed as compared with other evergreen broad-leaved spe-

Table 4. Basal area (BA) and relative basal area (RBA) of living trees in each quadrat. Values larger than 10% are underlined.

Vegetation type		*Dicranopteris* type				*Cyathea* type			
Quadrat		D1		D2		C1		C2	
Species	Abbriviation	BA $cm^2/100m^2$	RBA %	BA $cm^2/100m^2$	RBA %	BA $cm^2/100m^2$	RBA %	BA $cm^2/100m^2$	RBA %
Evergreen Coniferous trees									
Pinus luchuensis	*Pl*	715.6	48.67	920.7	71.14	1058.9	60.21	660.2	33.97
subtotal		715.6	48.67	920.7	71.14	1058.9	60.21	660.2	33.97
Evergreen broad-leaved trees									
Adinandra formosana	*Af*			1.0	0.08				
Antidesma japonicum	*Aj*	5.1	0.35						
Archidendron lucidum	*Al*			7.1	0.55				
Ardisia sieboldii	*As*	10.6	0.72			6.7	0.38	1002.0	51.56
Camellia sinensis	*Cs*							1.1	0.06
Cleyera japonica	*Cj*							23.7	1.22
Diospyros morrisiana	*Dm*	121.2	8.24			62.3	3.54		
Elaeocarpus japonicus	*Ej*	11.9	0.81					0.8	0.04
Eunonymus sp.	*Eu*	34.4	2.34						
Eurya acuminata	*Ea*					23.1	1.31		
Eurya japonica	*Ej*					25.6	1.46		
Ficus fistulosa	*Ff*					19.3	1.10	38.1	1.96
Ficus formosana	*Ffo*					0.9	0.05		
Glochidion rubrum	*Gr*	10.8	0.74						
Gordonia axillaris	*Ga*	30.9	2.10	44.2	3.41			0.8	0.04
Helicia cochinchinensis	*Hc*					11.4	0.65		
Itea oldamii	*Io*	1.1	0.07						
Lasianthus fordii	*Lf*	0.1	0.01					1.1	0.06
Lasianthus wallichii	*Lw*							1.0	0.05
Lindera communis	*Lc*							5.8	0.30
Litsea lotundifolia	*Ll*			3.1	0.24				
Machilus thunbergii	*Mt*			102.1	7.89				
Machilus zuihoensis	*Mz*			10.2	0.79	48.1	2.73	31.8	1.64
Maesa japonica	*Mj*					0.8	0.05	1.6	0.08
Melastoma candidum	*Mc*					3.2	0.18		
Michelia compressa	*Mco*	25.9	1.76			13.3	0.75	64.4	3.31
Myrsine seguinii	*Ms*	14.7	1.00						
Pithocerobium lucidum	*Plu*	121.2	8.24						
Prunus phaeosticta	*Pp*	188.1	12.79						
Randia cochinchinensis	*Rc*	51.4	3.50						
Sauranja oldhamii	*So*							1.4	0.07
Schefflera octophylla	*Soc*			8.0	0.62			43.2	2.22
Symplocos glauca	*Sg*					1.3	0.08		
Turpinia ternata	*Tt*					16.0	0.91		
Wendlandia formosana	*Wf*	30.5	2.08			268.6	15.27	6.4	0.33
subtotal		657.9	44.74	175.7	13.58	500.3	28.45	1223.1	62.93
Deciduous broad-leaved trees									
Aleurites cordata	*Ac*					23.0	1.31		
Clerodendrum cyrtophyllum	*Cc*	12.8	0.87	4.5	0.35	7.7	0.44	12.2	0.63
Ficus erecta var. *beecheyana*	*Fe*					0.8	0.04		
Fraxinus insularis	*Fi*			181.4	14.02				
Mallotus japonicus	*Mja*	62.4	4.25	3.1	0.24				
Mallotus paniculatus var. *paniculatus*	*Mp*	0.03	0.002			168.1	9.56	48.0	2.47
Rhus sylvestris	*Rs*			9.6	0.74				
Sapium discolor	*Sd*	21.7	1.47						
subtotal		97.0	6.59	198.7	15.35	199.6	11.35	60.2	3.10
Total		1470.4	100.00	1295.1	100.00	1758.8	100.00	1943.5	100.00

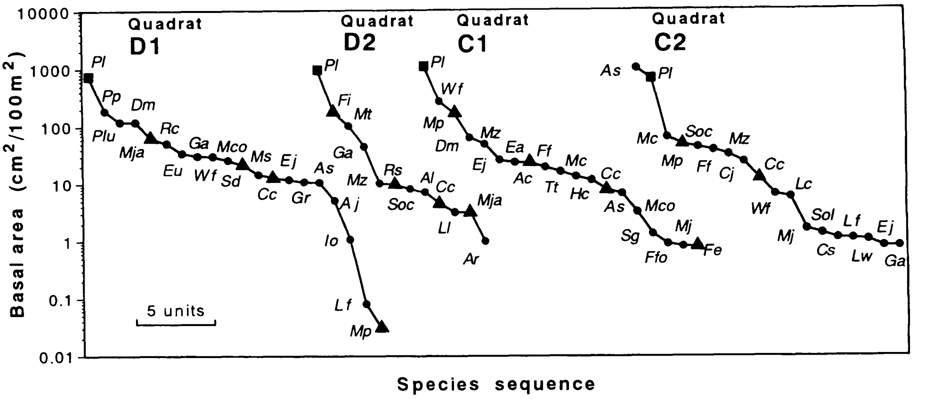

Fig. 5. Rank-abundance curves of living trees in each quadrat. Solid squares, circles and triangles represent *Pinus luchuensis*, evergreen broad-leaved species and deciduous broad-leaved species, respectively. See Table 4 for abbreviations of species name.

cies, because of their lower ability for seed dispersal.

In the Bonin Islands some pine forests are maintained after the pine wilt disease, because pioneer tall-tree species are absent except for *Pinus luchuensis* (Shimizu, 1987). *P. luchuensis* occupied the vacant niche in the islands, where there was no indigenous species with a growth form and physical feature like pine (Shimizu and Tabata, 1985). However, in Taiwan where the tree flora is far richer and sites suited for the natural regeneration of pine are limited, pine forests will be replaced by evergreen broad-leaved forest after the disease. Taoda (1988) also documented the succession from pine (*P. thunbergii*) forest to evergreen broad-leaved forest composed of indigenous species such as *Machilus thunbergii* after pine wilt disease on sand dunes of southern Kyushu.

Abrams and Scott (1989) documented a hypothetical example of the acceleration of succession by disturbance: in most cases, disturbance destroys part of the dominant pioneer overstory, which leads to an advance in reproduction of later successional species. Pine wilt disease accelerates the succession of pine forests to evergreen and/or deciduous oak forests in western Japan (Fujihara, 1996; Fujihara *et al.*, 1991). In Taiwan, the disturbance by pine wilt disease also seems to accelerate the succession from pine to evergreen broad-leaved forest.

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* Tentative translation by author.

台湾北部におけるマツ枯れ跡地の林分構造

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台湾北部におけるマツ枯れ跡地の林分構造を明らかにし，マツ枯れ後の植生遷移を推測した．調査地のマツ林は，種類組成からコシダタイプとヘゴタイプに区分された．個体数および基底断面積からみたマツ枯れ被害度は，コシダタイプで 62.8% および 80.2%，へ

ゴタイプで67.5％および61.6％であり，顕著な差は認められなかった．種数はヘゴタイプ（50および75種）の方がコシダタイプ（27および39種）より多かった．常緑広葉樹であるタブノキ，*Machilus zuihoensis*，フカノキおよび *Gordonia axillaris* などが両タイプの低木層に存在したが，ブナ科の木本はまれであった．台湾においてもマツ枯れによる攪乱後，マツ林から常緑広葉樹林への遷移は促進されると考えられた．