Progeny Differences of Hinoki (*Chamaecyparis obtusa*) and Sawara (*C. pisifera*) against Resinous Stem Canker Disease and Spatial Distribution of Damage (Disease Severity) in a Progeny Test

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The incidence and severity of resinous stem canker disease were investigated in hinoki (*Chamaecyparis obtusa*) and sawara (*C. pisifera*) at a progeny test located in Yamatsuri Town, Fukushima Prefecture, Japan. Symptoms of the disease were observed in 307 trees out of 933 investigated trees (32.9%). The damage was more severe on lower slopes than on upper slopes, indicating that microenvironmental factors are causally associated with the occurrence of the disease. The severity of the disease varied both among nine open-pollinated progenies derived from hinoki plus-tree clones and among 13 progenies derived from pollination between hinoki plus-tree clones and the mixed-pollen of hinoki plus-tree clones. The severity of the disease also varied with height above the ground. This tendency was most obvious where the disease was most severe. An estimation of the narrow sense heritability, h^2 , of 0.214, was obtained from analysis of the 13 progenies derived from pollination with mixed-pollen. The heritability derived from material that had not been subjected to selection against the disease, indicated that breeding to enhance resistance would be possible to control the disease. The interaction between environments and progenies in relation to severity of the disease is also discussed.

Key words: Chamaecyparis obtusa, Chamaecyparis pisifera, disease severity, heritability, hinoki stem canker disease

The occurrence of resinous stem canker disease has so far been observed in both hinoki (Chamaecyparis obtusa) and hiba (Thujopsis dolabrata) plantations in Japan. The damage caused by the disease causes economic losses through deterioration in woody quality. Great efforts have been made to identify causal agent(s) of the disease ever since Kitajima (1927) initially reported it. Although a number of possible causal agents, including both biotic and abiotic factors, have been proposed, the question of how the disease arises has yet to be resolved. Suzuki et al. (1988) and Yamaya et al. (1984) reported that abiotic stress factors such as cold and snowfall could be related to the incipient developmental stage of the disease. Some researchers have also reported that fungi such as Pezicula livida (Cryptosporiopsis abietina) (Kobayashi et al., 1990) and Cistella japonica (Suto, 1991, 1997) could be related to the development of the disease. Furthermore, Kusunoki et al. (1987) reported that wounds caused by the hinoki bark moth (Epinotia granitalis) could play a role by providing an entry point for various pathogenic fungi.

If there are non-random spatial distributions of damage caused by the disease in a tree and/or in a plantation, analysis of the spatial patterns should give important clues concerning the mechanism of the disease occurrence. The distribution of the disease has, therefore, been described in a range of hinoki plantations (Yamaya *et al.*, 1984; Kobayashi *et al.*, 1988; Suzuki *et al.*, 1988, Yanagita, 1993; Koiwa *et al.*, 1996; Takahashi *et al.*, 1997, 1998). For example, Kobayashi *et al.* (1988), Suzuki *et al.* (1988), and Takahashi *et al.* (1997, 1998) reported that damage caused by the disease was concentrated at a certain height at the lower part of the stems. Yamaya *et al.* (1984), Yanagita (1993), and Takahashi *et al.* (1997) reported that the severity of the disease in plantations was more severe on the lower slopes than on upper slopes. Takahashi *et al.* (1998) also reported that genetic factors affect the severity of the disease, according to an analysis of disease symptoms among hiba (*Thujopsis dolabrata*) provenances.

We have investigated a hinoki progeny test, where data regarding both the strains planted and their parental clones are available, to assess the relative importance of environmental and genetic factors in the occurrence of resinous stem canker disease. If environmental factors play a major role in the disease, improvements in the algorithms for selecting reforestation sites and/or management techniques in plantations should reduce its incidence. If genetic factors are largely responsible, breeding programs designed to enhance resistance could be an effective means of reducing it.

Materials and Methods

1 Investigated test and the mating design of the progenies

The incidence and severity of resinous stem canker disease were investigated in a progeny test located at Iriyama national forest, Yamatsuri Town, Fukushima Prefecture, in January 1997. This progeny test, consisting of three blocks with a total area of 0.63 ha, was set up in May 1974. The test is located on a southwestern slope the inclination of which ranges from 28 to 39 degrees. The altitude of the test ranges from 550 m to 610 m. Thirty-two progenies of hinoki (Chamaecyparis obtusa) and sawara (C. pisifera) were planted in the test as shown in Table 1. Plus-tree clones were used as mother trees for hinoki and sawara progenies. Progenies derived from pollination with two types of mixed-pollen were planted, as well as open-pollinated, and self-pollinated progenies. One of the pollen mixtures was collected from six hinoki plus-tree clones, Hakone 3, Nojiri 7, Tokyo 2, Minami-tama 4, Kataura 5, and Numazu 2 (referred to as mixed-1 in Tables 1 and 3).

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Table 1 I	List of prog	genies planted	l in the surve	yed progeny test
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No.	Mother tree of	Species of mother tree [†]	Mating ⁺⁺	Planted No. of each progeny Block		Surveye	Surveyed No. of each progeny		
	progeny	momer nee		T	DIOCK			Вюск	
				I	II	111	I	II	III
1	Utsunomiya 2	ob	mixed-1	15	15		15	11	
2	Kajikasawa 3	ob	mixed-1	15			14		
3	Ohtawara 2	ob	open	15	15	30	15	12	12
4	Ohtawara 2	ob	mixed-1	15	15	30	12	13	14
5	Kuji 7	ob	open	15			14		
6	Kuji 7	ob	mixed-1	15	60	75	13	9	14
7	Sakashita 3	ob	mixed-1	15	15		13	14	
8	Kuji l	ob	mixed-1	15	30	45	15	14	15
9	Tanzawa 7	ob	mixed-1	15	45	60	13	13	13
10	Tanzawa 7	ob	open	15	15		14	14	
11	Kuno 2	ob	mixed-1	15	15	30	12	12	15
12	Minamitama 3	ob	mixed-2	15	15	15	13	11	10
13	Minamitama 3	ob	self	15			11		
14	Tanzawa 8	ob	mixed-1	15			14		
15	Tanzawa 8	ob	open	15			14		
16	Kataura 6	ob	mixed-1	15	15	30	12	15	14
17	Kataura 6	ob	open	15	15		14	15	
18	Agematsu 4	ob	open	15			13		
19	Nojiri 7	ob	mixed-1	15	15	30	9	13	15
20	Nojiri 7	ob	open	15	15		14	13	
21	Bugi 3	ob	mixed-1	15			13		
22	Ena 2	ob	open	15			13		
23	Daigo-Exp. 6	ob	self	15			10		
24	Daigo-Exp. 6	ob	mixed-1	15	15	30	14	14	15
25	Daigo-Exp. 6	ob	open	15	15		14	14	
26	Daigo 1	pi	self	15	15		15	14	
27	Daigo 1	pi	open	15	15		14	14	
28	Daigo 2	pi	self	15	15		10	14	
29	Daigo 2	pi	open	15	15		13	14	
30	Ohtaki 102	pi	self	15	30	45	13	11	15
31	Ohtaki 102	pi	open	15	15		14	12	
32	Native hinoki	ob	uncertain	45	45	90	29	29	36

* ob and pi denote, *Chamaecyparis obtusa* (hinoki) and *C. pisifera* (sawara), respectively. ** The mixed-1 and mixed-2 denote pollination with mixed pollen of six hinoki clones and pollination with mixed pollen of hinoki and sawara clones, respectively. The details are described in "Investigated test and the mating design of the progenies."

The other type of the mixed pollen was a mixture of hinoki and sawara pollen (referred to as mixed-2 in Tables 1 and 3), but there was not detailed information about pollen donor clones. The designated numbers of the 32 progenies planted in the three blocks are also shown in Table 1.

2 Evaluation of damage

We investigated diameters at breast height (DBH) and severity of the disease among 933 trees representing 32 progenies planted in the test, as shown in Table 1. The heights were also measured of 205 trees (22.0%) chosen randomly from the three blocks, and the average height in each block was calculated from these values.

The individual damage index (IDI) and partial damage index (PDI) were determined according to criterion shown in Table 2. IDI was defined as severity of the disease in individual stems, from 0 to 4 m above the ground. The part of the stem was sub-divided into four zones: 0–1, 1–2, 2–3, and 3–4 m above the ground (referred to as four above-ground height classes in the following). The PDI was defined as the disease severity in each of these four zones, and the vertical

 Table 2
 Criteria of damage indices, and the number of trees damaged to each level in the three blocks.

Damage	Resin	Flat and/or	Block		
index	excretion sunken stem		Ι	II	III
0	None	None	251	214	161
1	From one site	None	43	30	13
2	From plural sites	None	83	40	10
3	Not considered ⁺	Cumulative damage to less than 50% of diameter	52	24	4
4	Not considered	Cumulative damage to more than 50% of diameter	7	1	0

⁺ The damage indices of 3 and 4 are defined only from the degree of flat and/or sunken stem.

distribution of damage was evaluated using the PDI data.3 Statistical analyses

The 32 progenies including the 13 hinoki mixed-pollen-pollinated progenies (referred to as "Mixed-C.ob.", No. 2 in Table 4), the nine hinoki open-pollinated progenies (referred Takahashi et al.

 Table 3
 Data sets of 66 progeny/block combinations used in ANOVAs.

Progeny No.	Mating [†]	Species [†]	Γ	Data type ^{††} Block	
			I	II	III
1	mixed-1	ob	а	а	
2	mixed-1	ob	а		
4	mixed-l	ob	а	а	а
6	mixed-1	ob	а	а	a
7	mixed-1	ob	а	а	
8	mixed-1	ob	а	а	а
9	mixed-1	ob	а	а	а
11	mixed-l	ob	а	а	а
14	mixed-1	ob	а		
16	mixed-1	ob	а	а	а
19	mixed-1	ob	а	а	а
21	mixed-1	ob	а		
24	mixed-1	ob	а	а	a
12	mixed-2	ob	d	d	d
3	open	ob	b	b	d
5	open	ob	b		
10	open	ob	b	b	
15	open	ob	b		
17	open	ob	b	b	
18	open	ob	b		
20	open	ob	b	b	
22	open	ob	b		
25	open	ob	b	b	
27	open	pi	с	с	
29	open	pi	с	с	
31	open	pi	с	с	
13	self	ob	d		
23	self	ob	d		
26	self	pi	d	d	
28	self	pi	d	d	
30	self	pi	d	d	d
32	uncertain	ob	d	d	d

⁺ See Table 1 for explanation of abbreviations. ⁺⁺ Letters denote that the data was used in the corresponding analyses. Details are described in "Statistical analyses" and Table 4.

to as "Open-C.ob.", No. 3) and the three sawara open-pollinated progenies (referred to as "Open-C.pi.", No. 4) were evaluated using the IDI data. A series of ANOVAs (the models shown in Table 4) were conducted to identify the principal factors related to the occurrence of the disease using the IDI values. The data sets used in the nine ANOVAs were differed, as shown in Tables 3 and 4. The factors included in the models of the "Mixed-C.ob." (No. 2), "Open-C.ob." (No. 3), and "Open-C.pi." (No. 4) analyses were the effects of blocks, progenies and the interaction between blocks and progenies. The effect of blocks was included in the "3-Block" (No. 1) analysis, and the effects of blocks, species, and the interaction between blocks and species were included in the "Species" (No. 5) analysis. Narrow sense heritability (h^2) was calculated using the formula, $h^2 = 4 * var(P) / \{var(P) + var(B*P) + \}$ ε ; where var (P), var (B*P), and ε denote the variance of progenies, the variance of the interaction between blocks and progenies, and the variance of errors within each progeny, respectively (Zobel and Talbert, 1984). Thus, IDI values were used for analyses 1 to 5 listed in Table 4. Four ANOVAs (Nos. 6, 7, 8, and 9 in Table 4) were also designed, using PDI

Table 4Models examined in nine ANOVAs and data sets included inthe analyses.

No.	Name of model	Model [÷]	Included data sets ^{††}
Indiv	vidual level	· · · · · · · · · · · · · · · · · · ·	
1	3-Blocks	$y = \mu + B + \varepsilon$	a, b, c, d
2	Mixed-C.ob.	$y = \mu + B + P + B^*P + \varepsilon$	а
3	Open-C.ob.	$y = \mu + B + P + B^*P + \varepsilon$	b
4	Open-C.pi.	$y = \mu + B + P + B^*P + \varepsilon$	с
5	Species	$y = \mu + B + S + B^*S + \varepsilon$	b, c
Unit	level		
6	3-Blocks (H)	$y = \mu + B + H + \varepsilon$	a, b, c, d
7	Mixed- $C.ob.$ (H)	$y = \mu + B + H + \varepsilon$	а
8	Open-C.ob. (H)	$y = \mu + B + H + \varepsilon$	b
9	Open-C.pi. (H)	$y = \mu + B + H + \varepsilon$	с

⁺ B, P, S, and H are abbreviations of block, progeny, species, and height above the ground, respectively. The μ , ε , B*P, and B*S denote average, error, the interaction between blocks and progenies, and the interaction between blocks and species, respectively. ⁺⁺ The data sets are shown in Table 3.

Table 5Summary of results of nine examined models.

No. Model		Factors ⁺							
	-	Block	Species	Progeny	Block* species	Block* progeny	Height		
Inc	tividual level								
1	3-Blocks	***							
2	Mixed-C.ob.	***		**		n.s.			
3	Open-C.ob.	*		***		**			
4	Open-C.pi.	n.s.		n.s.		n.s.			
5	Species	*	**		n.s.				
Ur	nit level								
6	3-Blocks(H)	***					***		
7	Mixed-C.ob. (H)	***					**		
8	Open-C.ob. (H)	***					*		
9	Open-C.pi. (H)	n.s.					n.s.		

⁺ n.s = non significant,* p < 0.05, ** p < 0.01, and *** p < 0.001.

values to determine, whether or not the damage severity varied vertically among four above-ground height classes.

The "glm" and "varcomp" procedures for SAS version 6.12 (SAS, 1988, 1996) were used for conducting ANOVAs and estimating variance components, respectively.

Results and Discussion

1 The relationship between micro-environmental factors and disease severity

The averages and standard deviations (SD) of heights and DBHs in the test were 10.98 ± 1.78 m and 10.97 ± 1.09 cm, respectively. Damage caused by the disease was observed on 185 out of 436 trees (42.4%) in block I, 95 out of 309 trees (30.7%) in block II, and 27 out of 188 trees (14.4%) in block III, as shown in Table 2. The total number of damaged trees was 307 out of 933 trees investigated (32.9%). The number of trees with flat and/or sunken stems (*i.e.* with a PDI of 3 or 4) was 59 in block I (31.9% of damaged trees, and 13.5% of all trees in the block), 25 in block II (26.3% and 8.1% of damaged and total trees, respectively), and 4 in block III (14.8% and 2.1%, of damaged and total trees respectively). The

averages and SDs of the PDI values were 1.00 ± 1.00 in block I, 0.76 ± 1.09 in block II, and 0.36 ± 0.80 in block III, respectively. Both incidence and severity of the disease were greater in blocks on the lower slopes than in blocks on upper slopes (Fig. 1). The effects of blocks were significant in seven out of nine ANOVAs (Table 5). Similarly, Yamaya et al. (1984) observed that damage increased from upper slopes to lower slopes, and from drier soils to wetter soils in 28 hinoki plantations located throughout the Tohoku District. Yanagita (1993) and Takahashi et al. (1997) also reported that damaged trees were more abundant on lower slopes of hinoki plantations in Fukushima Prefecture. Furthermore, Takahashi et al. (1998) reported that the disease severity differed according to location in a hiba (Thujopsis dolabrata) provenance test located in Aomori Prefecture, even though it is located at a flat site. The heterogeneous disease severity in the hiba provenance test could not be explained by cold and snowfall, but the authors suggested that the variation could be attributed to the heterogeneity of micro-environmental factors within the stand. Disease severity was quite variable in the progeny test examined in this study, too. Progenies derived from the same plus-tree clones showed differences in disease severity depending on the location of the blocks. The fact that genetically homogeneous materials showed differences in disease severity depending on location indicates that microenvironmental factors are causally to the disease.

2 Differences in degree of damage between two species

The IDI values in nine hinoki (*Chamaecyparis obtusa*) open-pollinated progenies were greater than those in three sawara (*C. pisifera*) open-pollinated progenies, and the difference was significant at the 1% level (Fig.2 and Table 5). Thus, although hinoki and sawara are taxonomically closely



Fig. 1 Individual damage indices of 933 trees from the three blocks in the investigated progeny test. Symbols shown in box denote damage indices.

related, they showed significantly different degrees of susceptibility to the disease. Further study of these two species might help elucidate mechanisms of spread and development of the disease through analysis of relevant morphological, physical, chemical, and physiological differences among tolerant hinoki clones, susceptible hinoki clones and sawara.

3 Vertical distribution of damage

Four ANOVAs including the effect of above-ground height effect in the models were performed. The differences in PDI values were found to be not significant among four aboveground height classes in the "Open-C.pi.(H)" analysis, but they were significant at the 5%, 1%, and 0.1% significance levels in the "Open-C.ob.(H)," "Mixed-C.ob.(H)," and "3-Blocks(H)" analyses, respectively (Table 5). Three "Open-C.pi." progenies having relatively low IDI values showed no significant differences among the above-ground height classes, but hinoki progenies with relatively high IDI values did (8 and 9 in Table 5). The differences among PDI values associated with the four above-ground height classes were clearer in block I, where the damage were most severe, than in block II and III (although the differences among the above-ground height classes were significant in all blocks; Fig. 3). Similarly, Takahashi et al. (1998) also observed that the differences



Fig. 2 Individual damage indices of *Chamaecyparis obtusa* (Open-*C.ob.*) and *C. pisifera* (Open-*C.pi.*) in blocks I and II. Average individual damage indices (IDI) with one standard error are presented. Numbers in the diagram denote sample number.



Fig. 3 Partial damage indices (PDI) of the four above-ground height classes in the three blocks.

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Fig. 4 Rate of trees classified into two different levels of disease severity of the four above-ground height classes in the three blocks.

among damage indices correlated with the above-ground height classes were significant in places where damage was intensive, but not in places where damage was less serious. These observations suggest that the damage tends to become more concentrated at a certain height above ground as the disease becomes more severe.

Rate of trees classified into 1 or 2 of PDI (it means damaged trees without abnormal-shaped stem) and rate of trees classified into 3 or 4 of PDI (it means damaged trees with abnormal-shaped stem) are presented in Fig. 4. Both rates were higher in blocks on the lower slopes than in blocks on upper slopes. Maximum values of both rates were observed at different above-ground height class in block III; at 1–2 m class in rate of trees with abnormal-shaped stem. Maximum values of both rates were observed at 0–1 m class in rate of trees with abnormal-shaped stem. Maximum values of both rates were observed at identical above-ground height class in other blocks; at 1–2 m class in block I and at 2–3 m class in block II. The vertical distributions of these two rates were well coincident with that of PDI (Figs. 3 and 4). It indicates that PDI was useful as one of measurements to evaluate the vertical distribution of damage severity of the disease.

4 Differences of sensitivity to the disease among progenies

The "Open-*C.ob.*" and "Mixed-*C.ob.*" data sets showed that the IDI values were significantly different among progenies at the 0.1% and at 1% levels, respectively (Figs. 5 and 6, and Table 5). However, the "Open-*C.pi.*" showed no significant differences among progenies. We believe that the variation could be attributed to a small number of progenies in the "Open-*C.pi.*" data set. The detection of significant differences among both "Mixed-*C.ob.*" and "Open-*C.ob.*" progenies indicates that the genetic factors are related to disease susceptibility. We obtained an estimation of narrow sense heritability, h^2 , of 0.214, based on the "Mixed-*C.ob.*" data set. Akashi *et al.* (1979) estimated the heritability (h^2) of resistance to nee-



Fig. 5 Individual damage indices of 13 *Chamaecyparis obtusa* progenies derived from the pollinations with mixed-pollen in the three blocks. Average individual damage indices (IDI) with one standard error are presented. Symbols "X" indicate that the progeny does not exist in the block.



Fig. 6 Individual damage indices of nine open-pollinated *Chamaecyparis obtusa* progenies in blocks I and II. Average individual damage indices (IDI) with one standard error are presented. Symbols "X" indicate that the progeny does not exist in the block.

dle cast disease resistance in Japanese larch (*Larix leptolepis*) to be 0.588, using progenies derived from plus-tree clones crossed with the mixed-pollen of the plus-tree clones and 0.047 using open-pollinated progenies of the plus-tree clones. Noguchi and Mikami (1985) estimated narrow sense heritability of the resistance to needle cast in Japanese red pine

(*Pinus densiflora*). They calculated h^2 to be 0.96 based on an inoculation experiment where 4×4 diallele cross progenies were used, and 0.36 based on the data obtained from open-pollinated progenies of the plus-tree clones under natural infection. The estimated heritabilities were somewhat different depending on the materials used in these studies. The estimated heritabilities of needle cast resistance in Japanese red pine were the highest, and in the study concerned, both obviously tolerant and extremely susceptible clones were also exposed to natural infection and included in the estimation. Although the hinoki and sawara trees investigated in our study were subject to natural infection and have not been selected for resistance against resinous stem canker disease at all, a h^2 value of 0.214 was estimated for the heritability. This indicates that the genetic factors might be as strong as those involved in needle cast resistance in Japanese red pine, and also suggests that genetic steps against the disease, i.e. breeding for resistance against resinous stem canker disease, may be effective. However, the ability to discriminate between tolerant and susceptible trees requires further research, because the disease mechanisms are still unclear at present. The mode of inheritance and the ratio of additive and non-additive inheritance variances should also be analyzed in detail in the future.

5 The interaction between environments and progenies

The effect of the interaction between blocks and progenies on the occurrence of the disease was not significant in the "Mixed-C.ob." and "Open-C.pi." data sets, but it was significant in the "Open-C.ob." data set at the 1% level (Table 5). The average IDI values were highest in block I and lowest in block III, as shown in Fig. 5. The "Mixed-C.ob." analysis did not show significant interaction between blocks and progenies. although four progenies (Nos. 4, 7, 8, and 16) included in the analysis showed highest IDI values in block II among three blocks (Fig. 5). The open-pollinated progeny derived from Kataura 6 (Progeny No. 17) was sole progeny that had higher IDI value in block II than in block I among "Open-C.ob." progenies (Fig. 6). The "Open-C.ob." analysis was conducted again, excluding the data appertaining to progeny No. 17, and the result showed no significant interaction effect between blocks and progenies. The "Open-C.ob." data set was based on the data from two blocks, and the data of four out of 18 progeny/block combinations involving these blocks were absent (22.2%). Because these considerations are likely to affect the results from the "Open-C.ob." analysis, we believe that the correlations are insufficiently strong to conclude that there is an interaction between blocks and progenies. It is noteworthy, however, that the mixed-pollen-pollinated progeny derived from Kataura 6 also showed the highest IDI value in block II. The Kataura 6 clone might, therefore, have unique properties associated with susceptiblity to resinous stem canker disease. The interaction between blocks and progenies demands study in greater detail in the future.

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