Forest canopy and community dynamics in a temperate old-growth evergreen broad-leaved forest, south-western Japan: a 7-year study of a 4-ha plot

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Summary

1 Forest canopy gap and community dynamics were studied in a 4-ha permanent plot of an old-growth evergreen broad-leaved forest dominated by *Castanopsis cuspidata* var. *sieboldii* and *Distylium racemosum* in the Tatera Forest Reserve, Tsushima Islands, south-western Japan. The forest was affected by a powerful typhoon in 1987 and was monitored from 1990 to 1997.

2 In 1990, all woody stems ≥ 5 cm diameter at breast height (d.b.h.) in the plot were identified, mapped and marked, and the state of 1600 5 m × 5 m contiguous quadrats used to locate canopy gaps. Gaps occupied 17.1% of the plot, which contained 4494 tree and shrub stems (total basal area 63.48 $m^2 ha^{-1}$). Gaps were re-censused in 1997 and both marked and newly recruited (≥ 5 cm d.b.h.) stems were recorded in 1992 and 1997.

3 Over 7 years the rates of canopy gap formation and closure were 0.72% $year^{-1}$ and 1.61% $year^{-1}$, respectively, mortality and recruitment rates were 0.97% $year^{-1}$ and 0.99% $year^{-1}$, and the rates of loss and gain in basal area were 0.95% $year^{-1}$ and 0.83% $year^{-1}$.

4 The mortality of stems was size-dependent, with those in middle size classes having the lowest rates. Mortality of stems was lower in canopy and higher in the understorey, while the proportion of stems killed by disturbances increased with height.

5 Stems that died during the 7 years were predominantly located in newly created gaps, whereas stems were recruited into both established and new gaps. Deciduous broad-leaved species were largely restricted to gaps that remained open throughout the study.

6 Both composition and structure of the forest changed in response to disturbance-related effects on canopy dynamics.

Key-words: disturbance, large plot study, long-term study, mortality, recruitment

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Introduction

Old-growth forests are heterogeneous in space and time and consist of patches at various stages of regeneration following gap formation (Watt 1947; Whitmore 1989). Populations of the constituent tree species are maintained and investigation of canopy and community dynamics in response to natural disturbance is needed to clarify the mechanism responsible (Runkle 1981, 1982; Canham 1989; Yamamoto 1992a, 1992b; Tanouchi & Yamamoto 1995).

The general characteristics and traits of a forest community cannot be detected by small-scale studies because heterogeneity in internal or external conditions, such as competition, topography, soil and light, are ignored. Short-term studies also give wrong estimates of forest canopy and community dynamics because the effects of rare or episodic events, such as large-scale or strong disturbances, are not considered. Large-scale and long-term studies of dynamics are therefore needed (Swaine *et al.* 1987; Bakker *et al.* 1996; Condit *et al.* 1996; Tanaka & Nakashizuka 1997), but although various forest types have been monitored (e.g. Phillips 1996; Nakashizuka *et al.* 1999),

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data from evergreen broad-leaved forests of Japan are restricted by the rarity of suitable old-growth forests.

Evergreen broad-leaved forest, which is found widely in humid areas at mid-latitudes in the northern hemisphere, is the natural vegetation of the warm-temperate zone in east Asia, where it is dominated by the families Fagaceae, Lauraceae and Hamamelidaceae (Kira 1991; Tagawa 1995). Such forests once covered most of the lowland and flat-hill area in south-western Japan, but old-growth stands today are found only around Shinto shrines, on islands and on steep mountain slopes unsuitable for human development. Remnants are small, at most a few hectares in size, scattered and rarely on level ground. However, Mount Tatera is regarded as holy and Tatera Forest Reserve is a truly primeval evergreen broad-leaved forest, covering *c.* 100 ha of flat or gently sloping land at low and middle elevation which has been strictly preserved since ancient times (Itow 1977, 1991).

Typhoons are the major agent of natural disturbance here (Naka 1982; Yamamoto 1992a; Bellingham *et al.* 1996), passing through or near the Tsushima Islands with high frequency (1.11 per year between 1951 and 1997, Manabe *et al.* 2000). Typhoon 12 created many new-canopy gaps in the reserve in 1987 and more than 10 typhoons have since passed through or near the site. These repeated disturbances gave us a good opportunity to monitor recovery following gap formation and to study regeneration and canopy dynamics in a primeval old-growth evergreen broad-leaved forest. A 4-ha permanent plot was established and canopy and tree censuses started in 1990 (for details of the physical conditions, species composition and stand structure of the plot, see Manabe *et al.* 2000).

We describe the patterns and processes involved in canopy dynamics of this old-growth forest from records of canopy gap formation and closure over 7 years. We investigate how the forest community and constituent tree species respond to disturbance-induced changes in the canopy, by evaluating tree demography (mortality and recruitment rates and their spatial pattern) and growth (loss and gain rate in basal area) in relation to canopy conditions. Finally, we compare our results with those from other old-growth forests.

Materials and methods

STUDY SITE

The Tatera Forest Reserve is located in the centre of the South Island of Tsushima (34° 25′ N and 129° 20′ E), between Kyushu Island, Japan, and the Korean Peninsula. The reserve is situated on the north-facing slope of Mount Tatera, between 120 m and 560 m above sea level, on ground that is steep only at high altitude. Annual mean temperature recorded close to the reserve is 15.1 °C, with monthly means ranging from 26.2 °C in August to 4.7 °C in January (data for 1961–90). Annual

precipitation is *c.* 2150 mm, heavier in June to September (more than 200 mm monthly); snowfall is rare.

The well-developed evergreen broad-leaved forest is dominated by *Castanopsis cuspidata* var. *sieboldii* and *Distylium racemosum* at low altitude and by *Quercus acuta* at high altitude (nomenclature follows Ohwi & Kitagawa 1983). On flat and gentle slopes at low altitude the canopy trees are over 1 m in diameter at breast height (d.b.h.) and over 25 m in height.

A powerful typhoon (typhoon no. 12) passed through the Tsushima Islands in August 1987 and damaged the forest in the reserve. Three of over 10 typhoons which passed through or near the reserve during 1990–97 were as powerful as typhoon 12 (two in 1991 and one in 1993).

TREE CENSUS

We set up a 4-ha (200 m × 200 m) permanent plot on flat ground or gentle slope between 120 m and 200 m a.s.l. and mapped all woody stems ≥ 5 cm d.b.h. in October 1990. Stems were mapped to the nearest 0.1 m, tagged and measured to the nearest 0.1 cm d.b.h. Each was characterized to species, state (living or dead) and canopy layer (I, canopy or subcanopy layer; II, ≥ 10 m tall but below subcanopy; III, < 10 m tall). Further censuses were carried out in autumn 1992 and 1997 and newly recruited stems ≥ 5 cm d.b.h. and dead stems were recorded. Woody vine stems ≥ 5 cm d.b.h. were recorded (*n* = 74) but only tree and shrub species were included in analyses.

CANOPY GAP CENSUS

In the autumn of 1990 and 1997 we estimated canopy gaps (*sensu* Runkle 1981) by eye, i.e. areas where canopy cover at over 10 m height was < 30% were considered to be in a canopy gap. Each 5 m × 5 m quadrat was distinguished as closed-canopy or canopy gap and, for the calculation of gap number and size, a gap was defined by its constituent set of 5 m × 5 m contiguous gap quadrats. Gap area was calculated by summing the number of gap quadrats. Gap formation and gap closure rates were determined from the number of quadrats whose status changed over the 7-year period. Gap closure could be due to the lateral expansion of the crowns of adjacent canopy trees or regeneration of individuals within the gap to a height of at least 10 m.

DATA ANALYSIS

Canopy dynamics were represented by:

$$\text{Gap fomation rate (\% year}^{-1}) = \frac{N_f}{N_t \cdot t} \times 100$$

$$\text{Gap closure rate (\% year}^{-1}) = \frac{N_c}{N_t \cdot t} \times 100$$

where N_f = the number of quadrats which changed from closed-canopy to canopy gap, N_c = the number of

quadrats which changed from canopy gap to closed-canopy, N_t = total number of quadrats (1600) and t = time interval.

In order to clarify the community dynamics, we estimated tree mortality rate, recruitment rate and rates of loss and gain of basal area (BA), using stem counts and BA values tallied into living, dead and newly recruited categories.

We estimated mortality and recruitment rates using a logarithmic model (Condit *et al.* 1995; Sheil & May 1996; Condit *et al.* 1999).

$$\text{Mortality rate (\% year}^{-1}) = \frac{\ln(N_b/N_s)}{t} \times 100$$

where N_b and N_s, respectively, are the number of stems alive at the beginning of the study and surviving to the end of the census period, and t is the time interval.

$$\text{Recruitment rate (\% year}^{-1}) = \frac{\ln(N_e/N_s)}{t} \times 100$$

where N_e and N_s, respectively, are the total number of the stems living at the end of the study and surviving throughout the census period.

To assess the statistical significance of any differences, confidence limits for the mortality and recruitment rate of each species and of the whole community were calculated using the normal approximation to the binomial variance, for all cases where at least five stems were recorded as dead or recruited, respectively. For smaller numbers, we calculated exact confidence limits using binomial probabilities. We created a table of 95% confidence limits for every combination of number of dead stems (D) and the number of stems at beginning of the study (N_0), and for each combination of number of recruits (R) and N_0, by searching for a population mean D^ or R^ for which the binomial probability of D or R being less than that chosen would be < 0.025; this was the upper 95% confidence limit (Sokal & Rohlf 1981) and a similar procedure was used for the lower confidence limit. Confidence limits were converted into annual mortality or recruitment rates using a logarithmic model.

We determined how much of the basal area was involved in mortality and recruitment.

$$\text{Loss of BA (\% year}^{-1}) = \frac{BA_l}{BA_b \times t} \times 100$$

where BA_l and BA_b are total BA of stems dying during the census period and of stems living at the beginning of the study.

$$\text{Gain in BA (\% year}^{-1}) = \frac{BA_g}{BA_e \times t} \times 100$$

where BA_g and BA_e are the BA values for stems recruited during the census period and living at the end of study.

Population changes for the main species were inferred from population growth rates (λ) (Condit *et al.* 1999) for stems and BA using data from 1990 and 1997:

$$\lambda_s(\% \text{ year}^{-1}) = \frac{\ln(N_{1997}/N_{1990})}{t} \times 100$$

or

$$\lambda_{BA}(\% \text{ year}^{-1}) = \frac{(BA_{1997} - BA_{1990})/BA_{1990}}{t} \times 100$$

where N and BA are the number of stems or the basal area of a species in a particular census.

The degree of dependence of dead or recruited stems on canopy gaps can be assessed by comparing their abundance beneath canopy gaps and beneath closed-canopy using a χ^2 test. The observed distributions were compared with those expected if stem status was randomly distributed over the plot. For dead stems in layer I, the expected number was less than five, and we therefore used Fisher's exact probability test.

Results

CANOPY GAP FORMATION AND GAP CLOSURE

In 1990, canopy gaps were scattered throughout the plot and represented 17.1% of the area (Fig. 1). By 1997- many of the small gaps which had existed in 1990 had disappeared (gaps reduced to 10.1% of area) but a very large gap had been formed to the right of the plot. Gap size distributions showed an inverse-J shape in both 1990 and 1997, although a continuous distribution across classes smaller than 500 m^2 in 1990 became discontinuous by 1997 (Fig. 2). In each year there was one gap larger than 1000 m^2, and while the total number of gaps decreased over the study (49 vs. 31), the area of the larger gap increased markedly (1075 vs. 1525 m^2).

Sixteen per cent of quadrats showed a change of status, with the number involved, and therefore the rate, being twice as high for gap closure as for formation (Table 1).
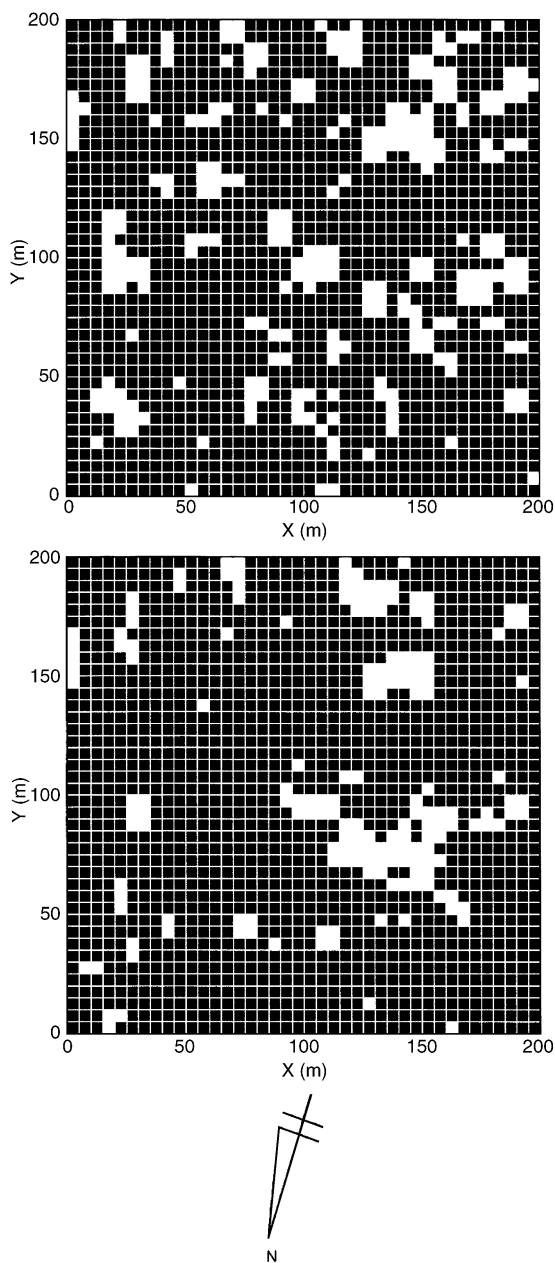
CHANGE IN STEM DENSITY

Overall, recruitment was similar to mortality (0.99% year^{-1} and 0.97% year^{-1} of total stems, Table 2), although total stem number was higher in 1992. Of the 145 stems recruited between 1990 and 1992, seven died by 1997 and were omitted from the analyses.
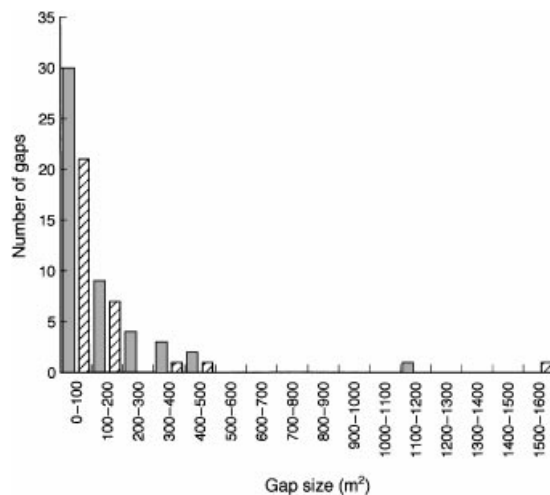
When annual mortality and recruitment rates were calculated (Table 2), the mortality rate was found to

Table 1 Change of canopy states over seven years

Canopy states	Quadrats (no.)	Rate (% year^{-1})
Gap → gap	94	
Gap → closed canopy (gap closure)	180	1.61
Closed canopy → gap (gap formation)	81	0.72
Closed canopy → closed canopy	1245	

Fig. 2 Gap size distribution in 1990 (solid shaded) and 1997 (hatched). The size of each gap was calculated as the sum of its constituent 5 m × 5 m quadrats.

be lower than the recruitment rate for the first 2 years but this trend was then reversed. Both recruitment and mortality rates were higher for the earlier census interval, but the difference was only significant for recruitment. When only canopy stems (layer I) were included, the mortality rate was 0.52% year^{-1}, i.e. lower than the gap formation rate.

CHANGE IN BASAL AREA

Losses in basal area in the 4-ha plot were only partially balanced by gains, although gains exceeded losses after 1992 (Table 3); overall rates were 0.95% year^{-1} and 0.83% year^{-1} for loss and gain, respectively. Most BA loss was due to the death of stems in layer I (82.6%) and most of the gain to growth of the surviving stems (94.1%, with remainder due to ingrowth). Canopy stem BA was lost at 1.06% year^{-1}, higher than the rate of gap formation.

SIZE-DEPENDENT MORTALITY

The diameter distribution of living stems changed little over the 7 years. For dead stems, numbers and

Fig. 1 Canopy states in 1990 (upper) and 1997 (lower). Each quadrat is 5 m × 5 m in area, and grey and white areas represent closed canopy and canopy gaps, respectively.

Table 2 Number of living, dead and recruited stems at each observation, and the rate of mortality, recruitment and 95% confidence limits during each census period

	Year or period	Stem (no. 4 ha^{-1})	Rate (% year^{-1})	95% confidence	limit
Living	1990	4494			
	1992	4533			
	1997	4498			
Mortality	1990–1992	106	1.19	1.42	0.97
	1992–1997	197	0.89	1.01	0.76
	1990–1997	296	0.97	1.08	0.86
Recruitment	1990–1992	145	1.63	1.89	1.36
	1992–1997	162	0.73	0.85	0.62
	1990–1997	300	0.99	1.10	0.87
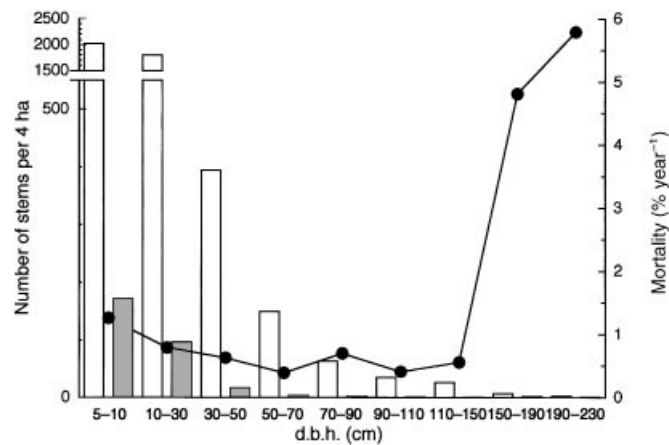
Fig. 3 Diameter at breast height class distribution (bars) and size-specific mortality (line). Open bars represent stems living in 1990, and shaded areas those stems which died during the 7 years.
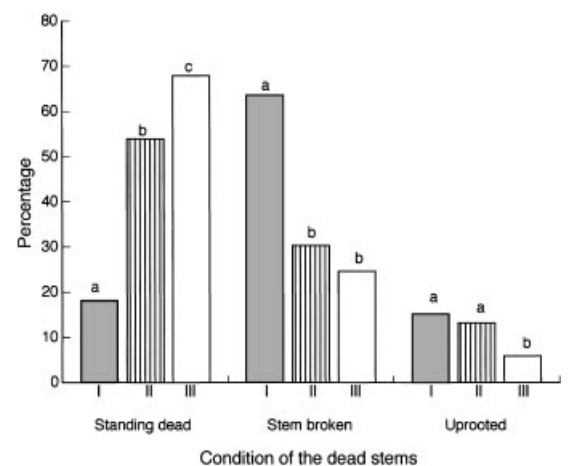
Table 3 Basal area (BA) of living stems, loss and gain in BA at each observation, the loss and gain rate in BA during each period

	Year or period	BA ($m^2 ha^{-1}$)	Rate (% $year^{-1}$)
Living	1990	63.48	
	1992	62.10	
	1997	62.93	
Loss (mortality)	1990–1992	2.60	2.05
	1992–1997	1.62	0.52
	1990–1997	4.22	0.95
Gain (growth & recruitment)	1990–1992	1.22	0.98
	1992–1997	2.44	0.78
	1990–1997	3.66	0.83

Fig. 4 The causes of stem mortality in each layer. Layer I is the canopy or subcanopy layer, layer II comprises individuals ≥ 10 m tall but not reaching the subcanopy, and layer III comprises stems < 10 m tall. Within each condition, values with a different letter are significantly different (normal distribution test, $P < 0.05$).

mortality showed different patterns across size classes (Fig. 3). Numbers decreased with increasing size, whereas mortality was least at intermediate size (50–70 cm and 90–110 cm diameter), increasing in both smaller and larger classes, but particularly above 150 cm diameter. Overall, increasing height in the canopy was associated with decreasing mortality (1.30, 0.78 and 0.52% $year^{-1}$ in layers III, II and I, respectively) and with death due to broken stems or uprooting rather than standing dead (Fig. 4). The high proportion of canopy stems whose death was due to breaking or uprooting (75.8%) implies that death was related to disturbance, such as the strong wind of typhoons.

### CHANGE IN SPECIES COMPOSITION AND DYNAMICS

Initially 35 tree and shrub species were present in the 4-ha plot, and a further two species appeared and one became locally extinct during the 7 years. Some species, however, showed considerable change in stem density or BA (Fig. 5). More than 70% of species showed little change in stem density (less than 2% $year^{-1}$), although some, but not all, rare species with small sample size changed markedly (pioneer species such as *Zanthoxylum*

ailanthoides and *Broussonetia papyrifera* had rates over 10% $year^{-1}$). Again many species (76.5%), including the most abundant, showed BA changes of < 2% $year^{-1}$, but rare species which either had large dead stems or were pioneers changed greatly.

The population dynamics of each of the 14 major species were characterized by the balance between mortality and recruitment and between loss and gain in BA (Table 4). We divided the species into three groups – large (maximum d.b.h. ≥ 100 cm), medium (100 cm > maximum d.b.h. ≥ 50 cm) and small (maximum d.b.h. < 50 cm) – but found few consistent patterns. Mortality was higher than recruitment in seven species and vice versa in the others but differences were only significant in *Dendropanax trifidus* and *Machilus thunbergii*. Small species tended to have larger loss and gain of BA than medium or large species. Of the codominant species in the stand, *Distylium racemosum* was decreasing in stem density but increasing in BA, whereas *Castanopsis cuspidata*
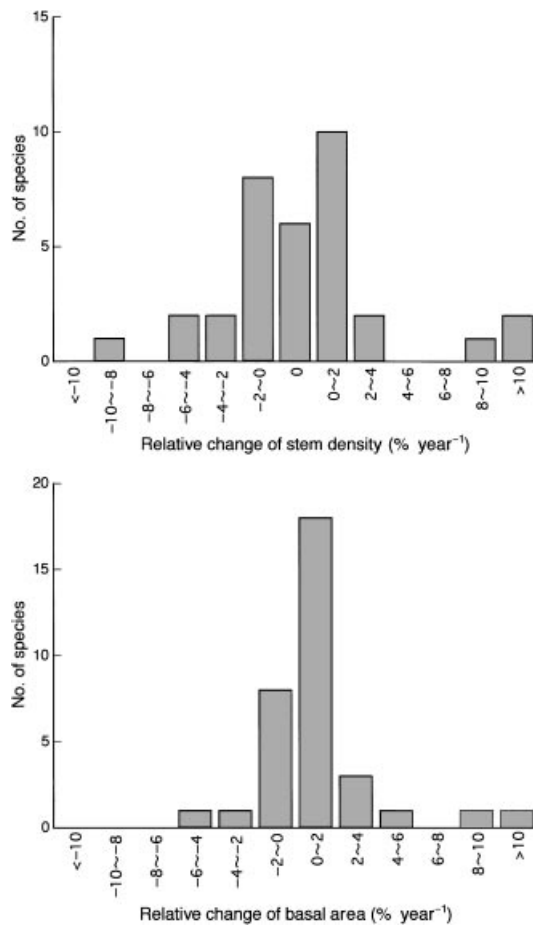
Fig. 5 The distribution of the relative change in stem density (upper) and BA (lower) of the 34 tree and shrub species present throughout the study.

var. *sieboldii* was increasing in stem density but decreasing in BA.

SPATIAL PATTERN OF MORTALITY AND RECRUITMENT

Both mortality and recruitment showed spatial heterogeneity (Fig. 6). Dead stems were concentrated in new gaps ($\chi^2 = 12.7$, $P < 0.001$) but not in older gaps ($\chi^2 = 1.8$, $P > 0.1$); however, the effect was due to layer II only (new gaps, $\chi^2 = 7.2$, $P < 0.01$, original gaps, $\chi^2 = 2.4$, $P > 0.1$, $P > 0.05$ for both classes in layers I and III).

Recruited stems were concentrated in both older ($\chi^2 = 24.4$, $P < 0.001$) and new gaps ($\chi^2 = 47.6$, $P < 0.001$). Few of the recruited stems (15/300) were of deciduous broad-leaved species but of these 13 recruited into gaps present at the start of the study.

Discussion

The canopy state changed remarkably over 7 years. The inverse-J shape seen in the gap size distribution in both 1990 and 1997 is consistent with many previous reports (e.g. Brokaw 1985; Yamamoto 1992a, 1995; Tanouchi & Yamamoto 1995; Kneeshaw & Bergeron 1998). Gaps are expanded by repeated disturbances (Runkle & Yetter

Table 4 Calculated annual rates of mortality, recruitment, loss and gain in BA and 95% confidence limits during 7 years of populations of the 14 major species

Species name	Stem density 1990 (no. 4 ha⁻¹)	Mortality (% year⁻¹)	95% confidence	limit	Recruitment (% year⁻¹)	95% confidence	limit	Basal area 1990 (m² ha⁻¹)	Loss in BA (% year⁻¹)	Gain in BA (% year⁻¹)	DBHmax 1997 (cm)
Castanopsis cuspidata var. sieboldii	166	1.45	2.18	0.76	2.44	1.57	3.38	24.88	1.52	0.74	210.7
Distylium racemosum	1642	0.59	0.73	0.45	0.46	0.34	0.59	20.47	0.22	0.81	142.1
Machilus thunbergii	62	6.26	9.18	3.84	1.68	0.28	3.24	0.92	0.41	0.85	114.4
Quercus salicina	54	2.29	3.98	0.78	0.31	0.00	0.94	4.63	1.15	0.55	103.9
Podocarpus macrophyllus	76	0.38	0.97	0.00	0.93	0.14	1.78	0.74	1.16	1.00	85.8
Dendropanax trifidus	143	1.04	1.69	0.41	0.11	0.00	0.32	1.51	0.33	1.23	67.3
Ternstroemia gymnanthera	69	0.85	2.00	0.00	1.06	0.16	2.02	0.77	0.41	0.43	61.3
Cleyera japonica	766	0.63	0.85	0.42	0.57	0.37	0.78	3.61	0.77	0.66	46.2
Camellia japonica	574	0.46	0.67	0.25	0.73	0.46	0.99	2.36	0.62	1.05	39.3
Neolitsea aciculata	112	2.35	3.52	1.27	4.70	3.25	6.31	0.33	2.95	3.01	37.8
Symplocos lucida	219	1.51	2.16	0.89	1.05	0.53	1.59	0.49	1.65	1.74	36.6
Cinnamomum japonica	118	2.51	3.68	1.42	1.89	0.93	2.92	0.35	2.47	2.53	25.2
Eurya japonica	145	1.34	2.09	0.63	1.73	0.93	2.58	0.18	2.21	1.84	18.8
Ligustrum japonica	98	1.70	2.74	0.73	2.13	1.06	3.30	0.12	1.75	1.78	16.6
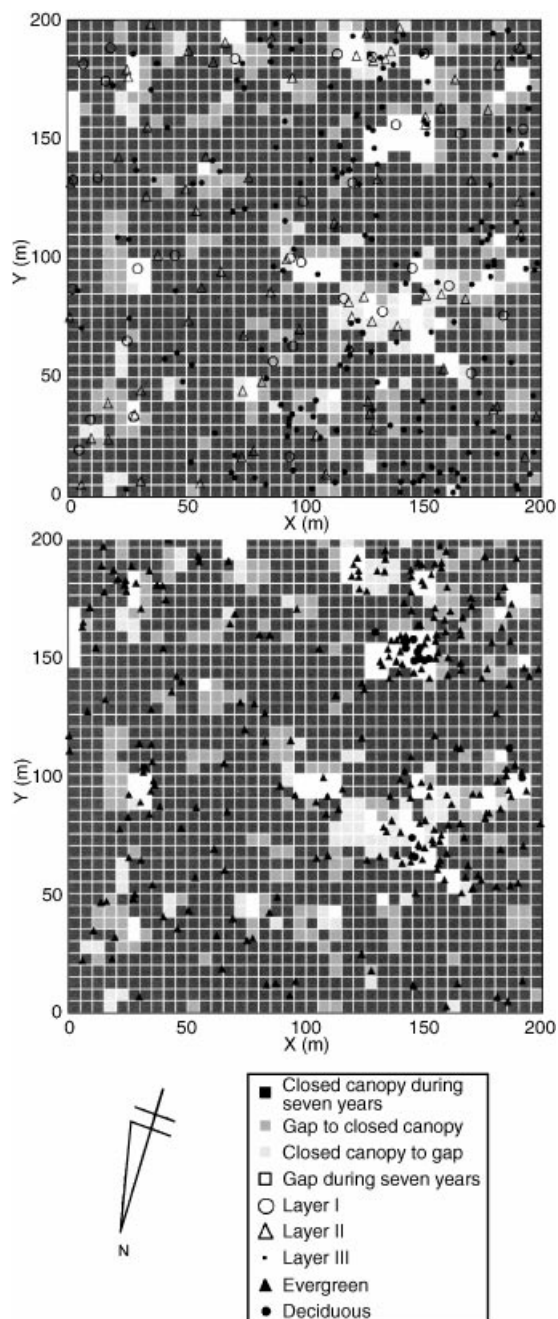
Fig. 6 Spatial distribution of dead (upper) and recruited (lower) stems in total.

1987; Tanaka & Nakashizuka 1997) and the several powerful typhoons that struck or passed near the Tsu-shima Islands might have caused both the observed gap formation and expansion. Gap closure was more frequent than gap formation, although we did not determine whether it was due to lateral expansion or regeneration within gaps. Thus, closed canopy seems to be maintained over the study plot as a whole, despite local dynamics, because canopy repair is more active than gap formation.

Annual gap formation rates of 0.2–1.26% have been reported in temperate forests (Naka 1982; Runkle 1982; Nakashizuka 1987; Tanaka & Nakashizuka 1997) and despite differences in the definition or measurement of

gaps our values fall in this range. Gap formation rates are similar for a variety of tropical and temperate forests (Runkle 1989), suggesting that they may vary little between mature forest types.

Overall changes in total stem density and basal area were small, with mortality more or less balancing recruitment (both about 1% year^{-1}) but with variation between the observation periods. Such variation is observed in many forests and often reflects natural disturbances (e.g. Burslem & Whitmore 1999; Marod *et al.* 1999; Masaki *et al.* 1999). The stem density of this plot increased during the first 2 years and then decreased, but temporal differences were significant only for recruitment: the reverse trend was observed for the basal area. When canopy trees died and gaps were formed by the strong typhoon in 1987, improved understorey light conditions are likely to have favoured new recruitment over mortality as seen in stem density changes in 1990–92, but competition, gap closure or new small-scale disturbances may then have caused increased mortality. Much of the change of basal area can be attributed to the fact that several large stems died between 1990 and 1992 but only one large stem died in the following 5 years. Both the frequency and intensity of disturbance were stronger in the first 2 years (two powerful typhoons in 1991) than subsequently (one typhoon) and changes in stem density and basal area in the sample plot during 7 years may reflect these events. Following typhoon 12, secondary succession may have been initiated in this forest with suppressed saplings growing and recruiting into d.b.h. ≥ 5 cm, but repeated disturbance probably stopped most recruitment and prevented succession from progressing to a later stage. Those stems which survived the repeated disturbance grew and contributed to the gain in basal area.

Various forest types have been reported to have recruitment and mortality rates of 0.5–7.7% year^{-1} and 0.5–3.8% year^{-1}, respectively (Lieberman & Lieberman 1987; Nakashizuka *et al.* 1992; Felfili 1995; Bellingham *et al.* 1999; Bunyavejchewin 1999; Burslem & Whitmore 1999; Marod *et al.* 1999; Masaki *et al.* 1999; Umeki & Kikuzawa 1999; Runkle 2000), as does this forest. The gain and loss rates for BA, however, fall outside those from other studies (1.11–1.82% year^{-1} and 0.88–1.85% year^{-1} in various forest types; Nakashizuka *et al.* 1992; Marod *et al.* 1999; Umeki & Kikuzawa 1999; Runkle 2000). This may be due to inclusion in other studies of only stems with d.b.h. ≥ 10 cm. Thus, community dynamics, like those of the canopy, may differ little between forest types.

Tree mortality is sometimes (Nakashizuka *et al.* 1992; Runkle 1998, 2000; Marod *et al.* 1999, and this study) but not always (Lieberman & Lieberman 1987; Swaine *et al.* 1987) size dependent. In addition, the proportion of mortality related to disturbance was higher in the uppermost layer. Small trees might be more vulnerable to shade under the closed canopy or to breakage by other falling stems, and thus show greater

mortality, whereas larger trees might be senescent, showing reduced vigour and, thus, less tolerant of natural disturbance, so that medium sized trees are favoured. Mortality by disturbance therefore appears to depend on tree size, and mortality will probably depend on the disturbance regime.

Although many species changed little over 7 years, some changed considerably. Few of the 14 major species showed a significant difference between mortality and recruitment, although one of the codominants, *Castanopsis cuspidata* var. *sieboidii*, tended to show higher recruitment because it forms many sprouts following stem damage during disturbance. However, less BA was gained than lost because of the death of several large stems over 1 m d.b.h. Some saplings of the other main species, including *Distylium racemosum*, recruited into ≥ 5 cm d.b.h., following repeated disturbance. The two species with significant differences, *Dendropanax trifidus* and *Machilus tunbergii*, both had higher mortality than recruitment but differed in major mortality factor (equal stem breakage and standing dead, respectively). Populations of individual species may change as a result of disturbance and suppression, with the balance between mortality and recruitment depending on canopy dynamics.

The patterns of dead and recruited stems show that both mortality and recruitment have spatial heterogeneity in relation to gap formation. Dead stems in upper layers were more likely to be in new gaps (particularly for layer II) and more likely to be due to stem breakage, suggesting that this is the mechanism by which disturbance creates gaps. In the lower layer (layer III) standing death was more likely than disturbance-related events and did not depend on gap age, suggesting that mortality here occurs irrespective of the presence or absence of disturbance. This vertical pattern may also reflect size-dependent mortality. Recruited stems were concentrated in both older and new gaps, due to growth of advanced saplings in gaps, where light levels are raised compared with under closed canopy (Canham 1989).

Sprouts from injured stems also play a role in maintaining populations in warm temperate forests (Bellingham *et al.* 1996) and were observed here for *Castanopsis cuspidata* var. *sieboidii*. Such regeneration does not depend on gap age, but most of the small number of deciduous broad-leaved species, such as *Zanthoxylum ailanthoides* and *Broussonetia papyrifera*, recruited into long-term gaps and rarely recruited under closed canopy. Such trees regenerate in gaps over 500 m^2 and this gap size rarely exists in many gap dynamic forests (Naka 1982; Brokaw & Scheiner 1989; Yamamoto 1992b). These species in the stand are thought to have 'pioneer' characteristics (Whitmore 1989) and, in evergreen broad-leaved forest, where the light condition under closed canopy is poor throughout the year, their seeds may germinate, but cannot establish and survive. In this plot, deciduous broad-leaved trees seem to regenerate in large gaps created by typhoon 12 in 1987 that have remained open or became further enlarged, and such sites may be needed for these species to regenerate and maintain their populations in old-growth evergreen broad-leaved forests.

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