Ecological Research (2004) **19**: 291–300

Effects of sika deer on tree seedlings in a warm temperate forest on Yakushima Island, Japan

Riyou TSUJINO[1]* and Takakazu YUMOTO[2]

[1]*Center for Ecological Research, Kyoto University, Kami-Tanakami-Hiranocho, Shiga 520–2113, Japan,* [2]*Research Institute for Humanity and Nature, 335 Takashima-cho, Marutamachi-dori Kawaramachi nishi-iru, Kyoto 602–0878, Japan*

High-density herbivore species often play an important role in forest regeneration. Native sika deer (*Cervus nippon yakushimae*) inhabit a high density (51.5–63.8 head/km^2, estimated by a pellet count method) area in the western part of a lowland natural forest on Yakushima Island, Japan. To test experimentally the impact of sika deer on the mortality and the survivability of current-year seedlings, which are at a more vulnerable stage than the later stages, we constructed fenced exclosures, planted seeds of nine sapfruit tree species and compared the mortality and the survivability of current-year seedlings between fenced and unfenced quadrats. Large seeded species had significantly greater survivability in fenced quadrats than in unfenced quadrats. However, the survivability disagreed with feeding preferences. Sika deer activity increased seedling mortality of large-seeded species more than that of small-seeded species, and did not decrease much seedling survivability of not-preferred species. We found that the physical disturbance by the high density of sika deer resulted in mortality for both preferred and not-preferred species, and that deer herbivory was important for preferred species.

Key words: current-year seedling; fence; mortality; seed size; sika deer.

Introduction

Mammals are thought to play important roles in determining vegetation structure (Shaw 1968; Griffin 1971; Kikuzawa 1988; McInnes *et al.* 1992; Ostfeld & Canham 1993; Ida & Nakagoshi 1996; Weltzin *et al.* 1997; Ickes *et al.* 2001; Wilby & Brown 2001). They do this, in particular, by affecting plant dynamics in various ways: for example, by seed predation (pig, Ickes *et al.* 2001; sika deer, Asada & Ochiai 1996); grazing and browsing (sika deer, Takatsuki & Gorai 1994; elk, Hobbs *et al.* 1981; snow hare, Pease *et al.* 1979); bark stripping (sika deer, Takatsuki 1990; Yokoyama *et al.* 2000); trampling (white-tailed deer, McCarthy & Facelli 1990) and digging into or otherwise disturbing the soil surface (pig, Bratton 1974; Ickes *et al.* 2001; grizzly bear, Tardiff & Stanford 1998).

Mammals can have a big impact on seedling survival and growth (Sork 1987; Myster & McCarthy 1989; Ostfeld & Canham 1993; Edwards & Crawley 1999), resulting in forests with fewer canopy trees and a well-developed understory of shrub and herbs (McInnes *et al.* 1992). This is because the critical events of plant development occur during the seed and seedling stages (Schupp 1995), with most seedling mortality occurring in the first growing season (e.g. Nakashizuka 1988). In order to clarify whether woody plants and forests can regenerate under a high population density of herbivore species, it is important to study the herbivore impact on current-year seedling, the most sensitive stage through the whole life history of trees.

Recently in Japan, natural vegetation has been reported as having been damaged because of feeding pressure by sika deer in places where they occur at high densities (e.g. Takatsuki & Gorai 1994). This study aimed to examine forests regenerate normally in a high population density of sika deer (*Cervus nippon yakushimae* Kuroda and Okada), focusing in particular on the establishment of current-year tree seedlings. We compared current-year seedling mortality and survivability between fenced seedling observation quadrats and unfenced quadrats. In addition, we estimated sika deer density by a pellet count method.

Materials and methods

Yakushima (30°20′N, 131°30′E) is a granite island surrounded by sedimentary rocks, located 70 km south of

*Author to whom correspondence should be addressed. Email: turi@ecology.kyoto-u.ac.jp

Received 5 June 2003, Accepted 1 October 2003.

Kyushu, Japan. We established a 50 × 50 m study plot in a warm-temperate evergreen broad-leaved forest on the western foot of Mt. Kuniwari (1323 m a.s.l.), approximately 270 m a.s.l. in April 2001. The study plot faced south-west and included a typical slope, from the ridge top to the valley. Granite is the parent rock of the whole study plot. The mean annual temperature and rainfall are approximately 21°C and 2600 mm, respectively (Tagawa 1980). The forest consists mainly of broad-leaved evergreen Fagaceae, Hamamelidaceae, Myrsinaceae, and Lauraceae. The maximum tree height is 12 m on ridge tops and 20 m in valleys (Noma 1997).

A subspecies of Japanese sika deer, *Cervus nippon yakushimae*, inhabit in the Yakushima Island, Japan. The subspecies, *C. n. yakushimae*, is endemic to Yakushima Island and also to Kuchierabujima Island, a small volcanic island 12 km north-west of Yakushima. The population density of *C. n. yakushimae* in the lowland forest on the western part of Yakushima Island has been estimated at 43–70 head/km^2 (Agetsuma *et al.* 2003), a density that might be high enough to result in damage to natural vegetation. Deer in the area experience no predation; natural predators are absent from the island, and hunting by humans is prohibited by law. In a broad-leaved evergreen forest in Japan, leaves and fruits of evergreen plants and graminoids are the primary food of sika deer (Takatsuki 1988; Takatsuki 1990; Asada & Ochiai 1996).

Tree census

We measured the d.b.h. of all living tree stems (d.b.h. ≥ 1 cm) in the 50 × 50 m study plot in 2001. We also checked bite marks of deer herbivory on understory vegetation of tree species (height ≥ 30 cm, d.b.h. < 1 cm) from November 2002 to May 2003. According to the bite marks, these individuals were categorized into three groups; (i) herbivored – obvious bite marks on the leaves; (ii) not-herbivored – no obvious bite marks on the leaves, and (iii) unclassified – some marks on the leaves, but we could not distinguish from the deer herbivory. If the number of positive individuals of particular species over the number of total individuals of the species is greater than 0.05, the species are defined as deer preferred species.

Seedling observation

In April 2002, we established two types of seedling observation quadrats, each with eight replicates within the 50 × 50 m study plot; fenced quadrats with planted seeds and unfenced quadrats with planted seeds. Two replicates of each type of quadrats were located on the ridge area, the upper slope, lower slope, and the foot slope. Deer neither nested nor dug into the soil in any of the study plot.

The fenced quadrats were 2 × 2 m, each one divided into 16 cells of 50 × 50 cm. The fence was 1.5 m high with a bottom half (< 1 m) of wire and a top half (> 1 m) of rope. In effect, the fence prevented deer from entering a 2.5 × 2.5 m area. However, Japanese macaque and rodents might have been able to penetrate the fence.

Not-fenced quadrats were 1.5 m^2, each one divided into four cells of 50 × 50 cm and four cells of 50 × 25 cm. Seeds were planted in the same density and same season as in the fenced quadrats.

We planted seeds of nine species: *Ardisia sieboldii* Miq. (Myrsinaceae), *Cleyera japonica* Thunb. p.p. emend. Sieb. et Zucc. (Theaceae), *Litsea acuminata* (B1) Kurata (Lauraceae), *Neolitsea aciculata* (B1) Koidz. (Lauraceae), *Neolitsea sericea* (B1) Koidz. (Lauraceae), *Symplocos prunifolia* Sieb. et Zucc. (Symplocaceae), *Syzygium buxifolium* Hook. et Arn. (Myrtaceae), *Ternstroemia gymnanthera* (Wright et Arn.) Bedd. (Theaceae), and *Vaccinium bracteatum* Thunb. (Ericaceae). These species are regionally abundant and comprise the lowland forest in Yakushima Island. We chose these species because of three reasons; (i) evergreen sapfruit species; (ii) they did not sprout much from trunks and, (iii) enough fruit were available. Although *V. bracteatum* sprouts much, we planted for the third reason. Mature fruit of each species was collected during 2001 or early 2002 from around the study area. Seeds were removed from the fruits, refrigerated (5°C) during the winter, and planted in early and late April 2002. The density of seeds planted in each quadrat is listed in Table 1.

We selected eight cells and four half-cells for fenced quadrats and four cells and four half cells for unfenced quadrats that were free of rocks and tree roots (which might affect seedling survival and growth). *Ardisia sieboldii*, *C. japonica*, *L. acuminata*, *Syn. prunifolia*, *Syz. buxifolium*, *T. gymnanthera,* and *V. bracteatum* were planted in a cell (0.25 m^2), and we replicated eight cells. However, *N. aciculata* and *N. sericea*, were planted in a half cell (0.125 m^2) for each species, and we replicated two half cells, because these two species were difficult to distinguish.

Seedling Dynamics

Tree seedlings that grew in the quadrats were identified and mapped. The emergence and survivorship of seedlings were censused at 10 days to 1 month intervals, from May 2002 to December 2002. Seedling death was classified into three terminal conditions; (i) standing dead – when the seedling died because of physiological reasons or had symptoms like a rotten stem or was a brownish color; (ii) vanished – when the seedling

Table 1 List of planted seeds

Species	Number of cells ($0.25\ m^2$) Fenced†	Unfenced†	Density seed/m^2 Both†
Ardisia sieboldii	8	4	52
Cleyera japonica	8	4	200
Litsea acuminata	8	4	36
Symplocos prunifolia	8	4	60
Syzygium buxifolium	8	4	40
Ternstroemia gymnanthera	8	4	52
Vaccinium bracteatum	8	4	80
Neolitsea aciculata‡	2	2	192
Neolitsea sericea‡	2	2	320

†'Fenced', 'Unfenced' and 'Both' indicate fenced quadrats ($8\ m^2$), unfenced ($1.5\ m^2$) quadrats, and both of them.
‡For *Neolitsea aciculata* and *Neolitsea sericea*, we planted seed in two of half-cells ($0.125\ m^2$) and the other seven species were mixed to be planted in eight cells ($0.25\ m^2$).

disappeared (presumably having been eaten by deer or washed out by soil surface erosion), and (iii) other – when the seedling died because of abiotic factors, such as soil disturbance or obstruction by fallen trees or leaves. The final census was conducted on 1 December 2002, at that time all living seedlings were classified as alive. The final survivability and mortality classifications were compared between fenced and unfenced quadrats.

We defined relative mortality rate as the ratio of the mortality in the fenced quadrat to that of unfenced quadrat, and relative survivability rate as the ratio of the survivability in the fenced quadrat to that of unfenced quadrat for each species.

In order to compare seed size, seedling size, and seedling mortality and survivability, we measured the wet weight of seeds. Such data was collected on at least 15 samples for each species, especially tiny seeds which were gathered at least 0.1 g in total to be measured. Current-year seedling heights of major species were measured for living seedlings during early October 2002.

Deer census by pellet count method

This study plot is situated apart from the study area of Agetsuma *et al.* (2003) and the forest types and topography are different. We also estimated sika deer density at the study plot by a pellet counting method, the most practical census method in an evergreen forest (Iwamoto *et al.* 2000).

We counted deer pellets using a method that had three main steps. First, we established six transects, 1×50 m each and 10 m apart. All deer pellets found within the transects were removed. Deer pellets were easily distinguished from other animal feces. Second, after a time interval Δt_1, we collected all the deer pellets within the transects, counted them, and placed them beside the transects. Third, after a time interval Δt_i, we repeated the second step but also counted the old deer pellets that had been placed beside the transects in previous censuses to estimate a pellet decay rate. This third step was repeated several times over a 2 or 3 week interval.

We conducted a total of seven censuses, first on 5–6 July 2002 and then on 18 July, 31 July, 8 August, 17 August, 5 September, and 19 September.

We estimated the density of sika deer as follows. When f' pellets are counted in area A after the interval Δt, f' is the number of pellets that AD heads of deer have dropped during Δt, where D is the density of deer per unit area. If a deer drops h pellets per unit time, the following equation is satisfied: $ADh\Delta t = f$, or

$$D = \frac{f'}{Ah\,\Delta t} \tag{1}$$

The pellet decay rate during our study was estimated by counting pellets. We defined the monthly pellet decay rate as the mean value of c, $(0 \le c < 1)$, calculated as follows:

$$c = 1 - (N/N_0)^{\frac{1}{\Delta t}} \tag{2}$$

where N_0 and N are the numbers of pellets at the start and end, respectively, of interval Δt.

We tried to minimize error in estimation by two ways. We conducted several censuses to avoid accumulating errors, and corrected them with an estimated pellet decay rate. If n is the number of total censuses, f_i' is the number of pellets found during the ith census, and Δt_i the duration of the ith census, the estimated density of sika deer will be

$$D = \frac{\sum f_i'}{Ah\sum \Delta t_i} \tag{3}$$

The estimated decaying duration for a pellet will be in the range of 0 to the interval Δt, and the mean will be half of the interval: $\Delta t/2$. So, the estimated mean pellet product of the ith census during Δt_i is $f_i = f_i' / (1-c)^{\frac{\Delta t_i}{2}}$, and the range is $f_i' \le f_i \le f_i' / (1-c)^{\Delta t_i}$. The estimated density of sika deer follows as

$$D = \frac{\sum f_i}{Ah\sum \Delta t_i} \tag{4}$$

Because D is between the maximum and minimum consideration of pellet decay rate, the range of the estimated density will be $\dfrac{\sum f_i'}{Ah\sum \Delta t_i} \le D \le \dfrac{\sum f_i'/(1-c)^{\Delta t_i}}{Ah\sum \Delta t_i}$

In the present study, we assumed that $h = 30$ 300 pellets/month (Takatsuki *et al.* 1981).

Results

There were 1934 tree stems and 34 tree species (d.b.h. ≥ 1 cm) in the study plot. Fagaceae, Hamamelidaceae, and Theaceae were popular groups (Table 2). There were 34 tree and shrub species (height ≥ 30 cm, d.b.h. < 1 cm) in the study plot. Symplocaceae, Myrsinaceae, and Theaceae were popular groups (Table 3). A histogram of tree abundance is shown in Fig. 1. Seedlings of 34 tree species germinated during the census period, including three unidentified woody species. Eight tree species, *Syz. buxifolium*, *V. bracteatum*, *L. acuminata*, *N. aciculata*, *N. sericea*, *Eurya japonica* Thunb., *C. japonica*, and *Schefflera octophylla* (Lour.) Harms, germinated more than 50 seedlings in total. Fewer than 50 seedlings germinated for *T. gymnanthera* and *Sym. prunifolia*, though seeds of these species were planted, and more than 50 seedlings of *E. japonica* and *Sc. octophylla* – which were not planted – germinated. Figure 2 describes the seedling dynamics of tree species in fenced and unfenced quadrats, including both planted and not-planted species.

More than 5% of understory vegetation individuals of nine tree species and three shrub species had bite marks on their leaves, and we judged them as deer preferred species. Eighteen tree species and four shrub species were not judged as deer preferred species. (Table 3).

Although *A. sieboldii* also had more than 50 seedlings germinate, half of the total number of seedlings died of misgermination. They died before they would have

Table 2 Number of stems, sum of basal area, and maximum d.b.h. in the study plot (2500 m^2), and germinated seedlings in fenced (32 m^2) and unfenced quadrats (12 m^2) before 1 December 2002

Family	Species	Life form	No. stems (d.b.h>=1 cm)	BA (cm^2)	Max d.b.h. (cm)	Seeding no. Fenced	Unfenced
FAGAC.	*Quercus salicina*	ET	77	35159.43	75.8	7	1
HAMAMELIDAC.	*Distylium racemosum*	ET	206	31571.49	52.8	1	0
FAGAC.	*Quercus phillyraeoides*	ET	5	18331.07	108.5	0	0
FAGAC.	*Pasania edulis*	ET	118	15267.60	34.4	0	0
SYMPLOCAC.	*Symplocos prunifolia*	ET	69	11201.99	32.5	11	1
THEAC.	*Cleyera japonica*	ET	189	10792.49	31.5	273	75
MYRSINAC.	*Myrsine seguinii*	ET	300	9035.42	19.6	2	0
ERICAC.	*Rhododendoron tashiroi*	ET	230	8705.10	31.2	20	5
MYRSINAC.	*Ardisia sieboldii*	ET	87	6434.23	36.4	176	109
FAGAC.	*Castanopsis sieboldii*	ET	5	6170.25	70.3	0	0
THEAC.	*Ternstroemia gymnanthera*	ET	74	5845.09	43.3	2	5
LAURAC.	*Litsea acuminata*	ET	14	5304.22	39.	385	131
LAURAC.	*Neolitsea aciculata*	ET	30	5078.13	39.5	71	22
ARALIAC.	*Schefflera octophylla*	ET	12	4046.02	30.4	384	126
ERICAC.	*Vaccinium bracteatum*	ET	26	3569.53	30.4	87	26
THEAC.	*Camellia japonica var. macrocarpa*	ET	88	3529.07	20.4	1	0
THEAC.	*Eurya japonica*	ET	99	3419.47	15.9	204	47
MYRTAC.	*Syzygium buxifolium*	ET	29	1970.31	19.6	470	234
MYRICAC.	*Myrica rubra*	ET	16	1932.42	25.9	0	0
LYTHRAC.	*Lagerstroemia subcostata*	DT	5	1086.01	36.9	30	4
EUPHORBIAC.	*Aleurites cordata*	DT	97	1021.06	14.3	0	0
LAURAC.	*Neolitsea sericea*	ET	6	661.35	22.8	34	19
DAPHNIPHYLLAC.	*Daphniphyllum teijsmannii*	ET	3	616.90	22.0	3	1
THEAC.	*Camellia sasanqua*	ET	23	393.82	14.6	0	0
EBENAC.	*Diospyros morrisiana*	ET	4	254.23	12.3	2	1
MYRSINAC.	*Maesa tenera*	Esh	80	242.39	5.7	35	6
AQUIFOLIAC.	*Ilex goshiensis*	ET	7	215.16	12.7	26	6
SYMPLOCAC.	*Symplocos glauca*	ET	26	119.87	4.6	0	0
ELAEOCARPAC.	*Elaeocarpus sylvestris*	ET	1	49.74	8.0	0	0
PROTEAC.	*Helicia cohinchinensis*	ET	2	10.24	3.0	0	0
AQUIFOLIAC.	*Ilex rotunda*	ET	2	6.71	2.4	2	1
SYMPLOCAC.	*Symplocos lucida*	ET	2	5.17	2.2	0	0
EUPHORBIAC.	*Mallotus japonicus*	DT	1	3.06	2.0	1	0
EBENAC.	*Diospyros japonica*	DT	1	2.15	1.7	0	0
	Total	1934	192051.22				

(BA), Basal area; (DT), Deciduous tree; (ET), Evergreen tree; (Esh), Evergreen shrub.

Table 3 No. individuals (height ≥ 30 cm, d.b.h. < 1 cm) in the study plot (2500 m^2) and ratios of deer preference of each species (= no. herbivored individuals over total no. species)

			No. sapling individuals hervibored or not				
Family	Species	Life form	H	N	Uc	Total	Deer preference
RUBIAC.	*Psychotria rubra*	Esh	130	53	0	183	0.71
EBENAC.	*Diospyros morrisiana*	ET	2	1	0	3	0.67
MYRSINAC.	*Ardisia sieboldii*	ET	43	26	4	73	0.59
PROTEAC.	*Helicia cohinchiensis*	ET	1	1	0	2	0.50
MYRSINAC.	*Myrsine seguinii*	ET	164	228	4	396	0.41
LAURAC.	*Litsea acuminata*	ET	44	85	0	129	0.34
LAURAC.	*Neolitsea sericea*	ET	4	9	0	13	0.31
MYRICAC.	*Myrica rubra*	ET	7	15	1	23	0.30
MYRSINAC.	*Maesa tenera*	Esh	17	165	12	194	0.09
LAURAC.	*Neolitsea aciculata*	ET	1	11	0	12	0.08
RUBIAC.	*Damnancathus indicus*	Esh	3	35	0	38	0.08
THEAC.	*Ternstroemia gymnanthera*	ET	1	14	2	17	0.06
ERICAC.	*Rhododendoron tashiroi*	ET	2	38	2	42	0.05
ROSAC.	*Rubus sieboldii*	Esh	1	24	1	26	0.04
SYMPLOCAC.	*Symplocos glauca*	ET	1	38	2	41	0.02
THEAC.	*Cleyera japonica*	ET	1	40	0	41	0.02
SYMPLOCAC.	*Symplocos prunifolia*	ET	5	1017	35	1057	0.00
THEAC.	*Eurya japonica*	ET	0	427	5	432	0.00
HAMAMELIDAC.	*Distylium racemosum*	ET	1	278	5	284	0.00
THEAC.	*Camellia japonica* var. *macrocarpa*	ET	1	131	0	132	0.01
MYRTAC.	*Syzygium buxifolium*	ET	0	118	2	120	0.00
EUPHORBIAC.	*Aleurites cordata*	DT	0	48	5	53	0.00
THEAC.	*Camellia sasanqua*	ET	0	43	2	45	0.00
ROSAC.	*Rubus grayanus*	Esh	0	44	0	44	0.00
SYMPLOCAC.	*Symplocos lucida*	ET	0	25	1	26	0.00
EUPHORBIAC.	*Glochidion obovatum*	DT	0	6	1	7	0.00
AQUIFOLIAC.	*Ilex liukiuensis*	ET	0	3	0	3	0.00
CALLICARPAC.	*Callicarpa shikokiana*	DSh	0	3	0	3	0.00
FAGAC.	*Pasania edulis*	ET	0	3	0	3	0.00
EUPHORBIAC.	*Mallotus japonicus*	DT	0	2	0	2	0.00
AQUIFOLIAC.	*Ilex goshiensis*	ET	0	1	0	1	0.00
AQUIFOLIAC.	*Ilex rotunda*	ET	0	1	0	1	0.00
MYRSINAC.	*Ardisia crenata*	Esh	0	1	0	1	0.00
STYRACAC.	*Styrax japonica*	DT	0	1	0	1	0.00
Total			429	2935	84	3448	0.12

(BA), Basal area; (DT), Deciduous tree; (ET), Evergreen tree; (Esh), Evergreen shrub. (H), Herbivored individuals; (N), not-herbivored individuals; (Uc), unclassified individuals.

opened their first leaves, so this species was not included in the analyses.

The remainder of this paper focuses on eight tree species, each of which had more than 50 seedlings germinate: *L. acuminata*, *N. sericea*, *Syz. buxifolium*, *N. aciculata*, *Sc. octophylla*, *C. japonica*, *V. bracteatum*, and *E. japonica*. We abbreviated these species as La, Ns, Sb, Na, So, Cj, Vb, and Ej, respectively.

According to the bite mark census on the understory vegetation, La, Ns, and Na were deer preferred species, and Sb, Cj, and Ej were not-preferred species (Table 3). Because younger stages of So and Vb were not detected in the study plot, we judged their preference another way. We observed that fallen branches with leaves of So were usually removed by deer immediately. All Vb individuals in the study plot had bite marks on their sprouts. Thus, five species – La, Na, Ns, So, and Vb – were preferred species, and the other three – Sb, Cj, and Ej – were not-preferred species.

The survival of four species—La ($p < 0.001$, binominal-test), Ns ($p < 0.05$), Sb ($p < 0.01$), and So ($p < 0.01$)—was significantly higher in the fenced quadrats than in the unfenced quadrats (Fig. 2). Furthermore, all eight species had higher survival rates in the fenced quadrats throughout most of the observation period.

The dead condition of seedlings during the study period showed different composition between the fenced and unfenced quadrats (Fig. 3). The ratio of vanished death were greater in the unfenced quadrats than in fenced quadrats for most species, except for Sb, and the ratios of standing dead were greater in the fenced quadrats than in unfenced quadrats, except for Vb. The composition was significantly different between fenced and unfenced quadrats for La (x^2 -test, d.f. = 2, p = 0.001), and So (x^2 -test, d.f. = 2, p < 0.01). The relative mortality rate did not differ significantly between four of the preferred species and three of the others (Mann–Whitney's U-test, U = 5, p = 0.456, n = 8). The seed weight of each species was significantly correlated with the relative mortality rate (Spearman's rank correlation test, rs = 0.976, p < 0.01, n =8, Fig. 4).

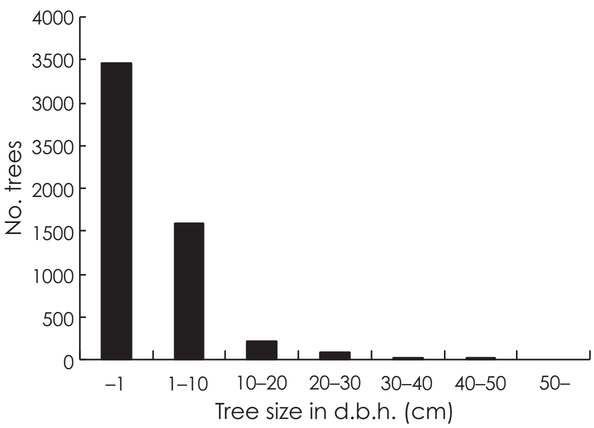

Fig. 1. Histogram of tree individual abundance in each d.b.h. classes. All tree and shrub individuals in the study plot (2500 m^2) were classified into 7 degrees; 30 cm height to 1 cm in d.b.h., 1–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, and over 50 cm in d.b.h.

The relative survival rate did not differ significantly between four of the preferred species and three of the others (Mann–Whitney's U-test, U = 11, p = 0.077, n = 7). Vb were not examined because of zero survivability. And, seed weight of each species was not significantly correlated with the relative survivability rate (Spearman's rank correlation test, rs = -0.429, p = 0.294, n = 7, Fig. 5).

The mean wet weight of seed and seedling heights were correlated significantly (Spearman's rank correlation coefficients test, rs = 0.976, p < 0.01, n = 8, Fig. 6).

The detected number of deer pellets and the estimated maximum production of deer pellets in the study area (A = 0.0003 km^2) are shown in Table 4. The total study period was 75.5 days. The estimated decay rate of deer pellets was $c = 0.37 \pm 0.06$ (mean ± SEM,

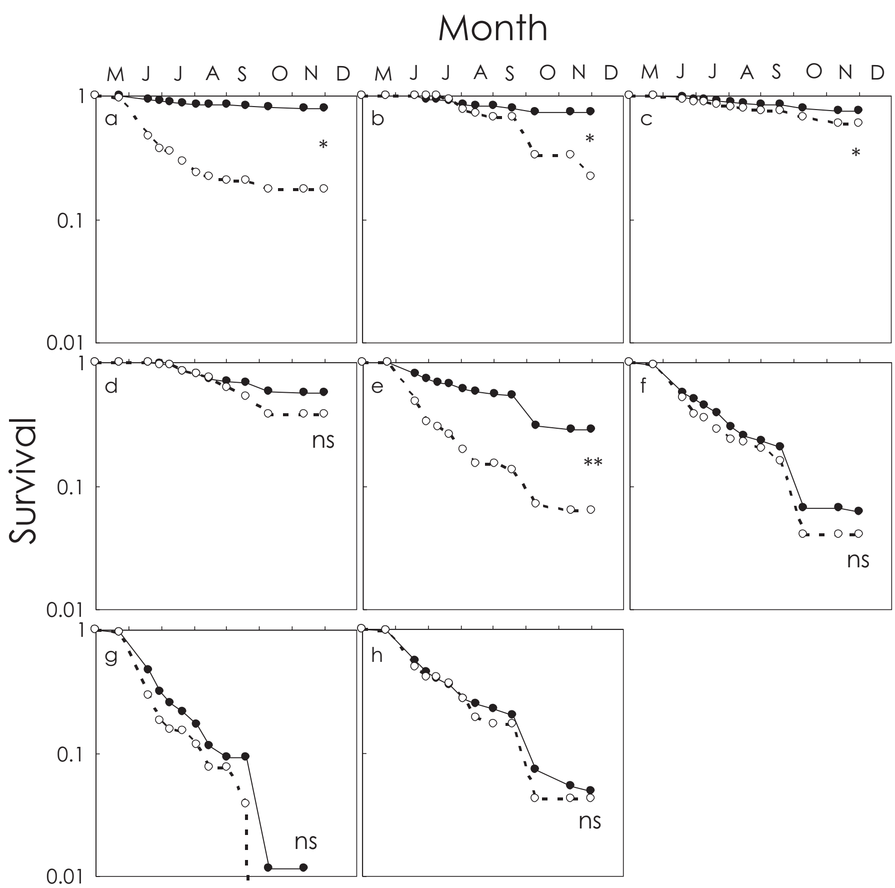

Fig. 2. Seedling survivability of tree species in fenced and unfenced quadrats from 1 May 2002 to 1 December 2002. Figure shows the significance of levels in the differences of survivability between the fenced and unfenced quadrats. (●), fenced; (○), unfenced. (*), p <0.05; (**), p <0.01; (ns), not significant (binominal test). (a), *Litsea acuminata*; (b), *Neolitsea sericea*; (c), *Syzigium buxifolium*; (d), *Neolitsea aciculata*; (e), *Schefflera octophylla*; (f), *Cleyera japonica*; (g), *Vaccinium bracteatum*; (h), *Eurya japonica*.

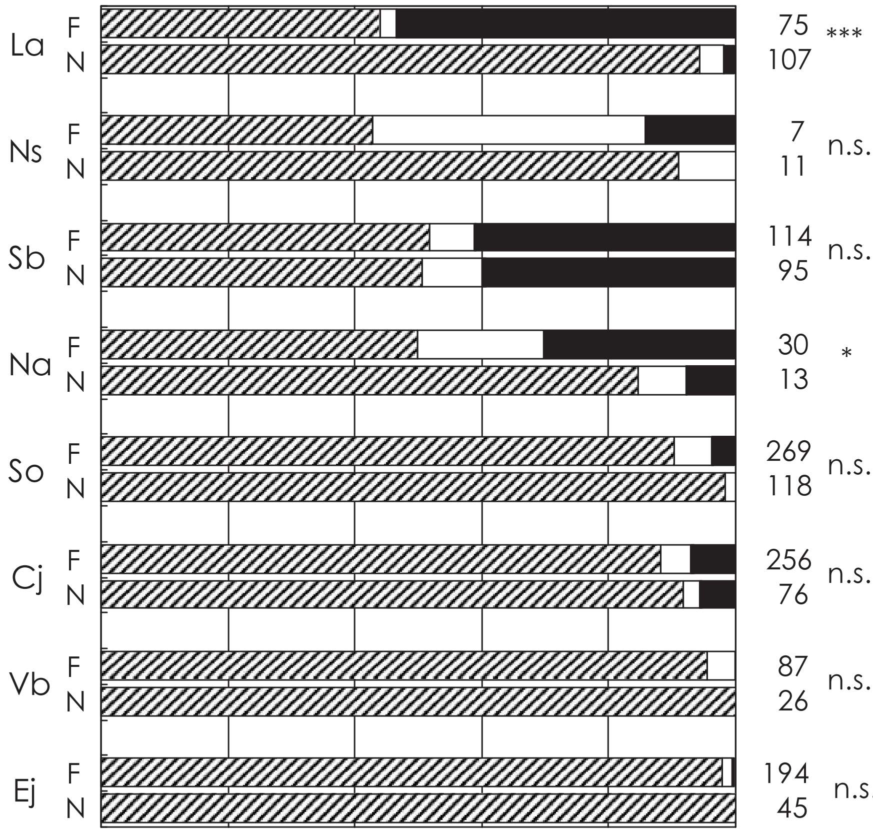

Fig. 3. Ratios of the dead conditions of seedlings in eight tree species. (Cj), *Cleyera japonica*; (Ej), *Eurya japonica*. (La), *Litsea acuminata*; (Na), *Neolitsea aciculata*; (Ns), *Neolitsea sericea*; (Sb), *Syzygium buxifolium*; (So), *Schefflera octophylla*; (Vb), *Vaccinium bracteatum*. (F), fenced quadrats; (N), unfenced quadrats; (*), $p < 0.05$; (***), $p < 0.001$; (ns), not significant (x^2-test); (▨), vanished; (□), other reason; (■), standing dead.

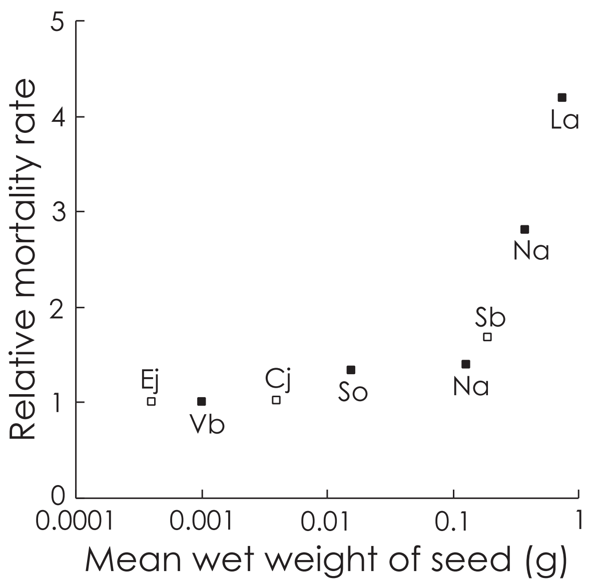

Fig. 4. Relationship between mean wet weight of seed and the relative mortality rate (= mortality in unfenced quadrat over mortality in fenced quadrat). (Cj), *Cleyera japonica*; (Ej), *Eurya japonica;* (La), *Litsea acuminata*; (Na), *Neolitsea aciculata*; (Ns), *Neolitsea sericea*; (Sb), *Syzygium buxifolium*; (So), *Schefflera octophylla*; (Vb), *Vaccinium bracteatum*. (■), preferred species; (□), not-preferred species.

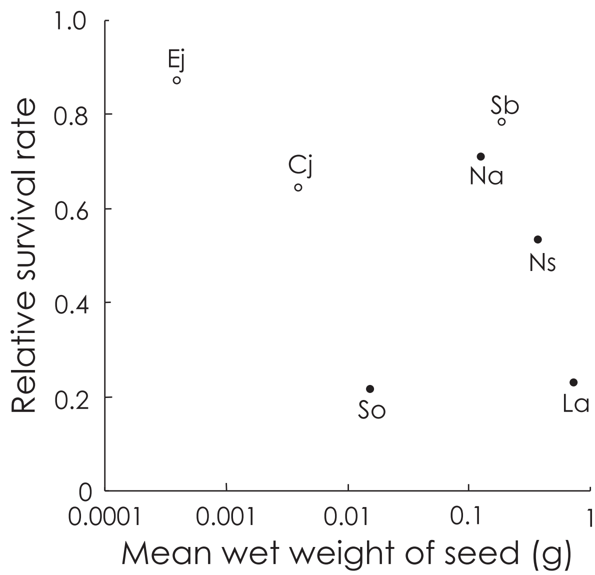

Fig. 5. Relationship between mean wet weight of seed and the relative survivability rate (= survivability in unfenced quadrat over survivability in fenced quadrat). (Cj), *Cleyera japonica*; (Ej), *Eurya japonica;* (La), *Litsea acuminata*; (Na), *Neolitsea aciculata*; (Ns), *Neolitsea sericea*; (Sb), *Syzygium buxifolium*; (So), *Schefflera octophylla*. (●), Preferred species; (○), not-preferred species. *Vaccinium bracteatum* was not shown as it did not survive.

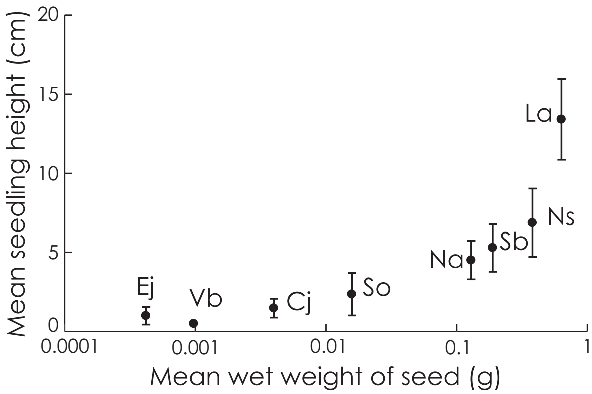

Fig. 6. Relationship between mean wet weight of seed and current-year seedling height (mean ± SD) in the fenced quadrat. (Cj), *Cleyera japonica*; (Ej), *Eurya japonica;* (La), *Litsea acuminata*; (Na), *Neolitsea aciculata*; (Ns), *Neolitsea sericea*; (Sb), *Syzygium buxifolium*; (So), *Schefflera octophylla*; (Vb), *Vaccinium bracteatum*.

n = 22). We counted 1162 pellets in total, and the estimated maximum production was 1439.2 pellets. Thus, the estimated deer density was in the range of 51.5–63.8 head/km^2.

Discussion

Deer density and vegetation shift

Our estimates of deer density – 51.5–63.8 head/km^2 – were greater than those in other areas, for instance 22.4–37.9 head/km^2 on the Boso peninsula, central Honshu (Ochiai & Asada unpubl. data, cited from Asada & Ochiai 1996). Furthermore, the estimate was nearly equal to that of Kinkazan Island, northern Japan, where deer inhabit in high density (60 head/km^2) and is well known that young trees are killed by sika deer (*C. nippon*) browsing in the deciduous forest (Takatsuki & Gorai 1994). Thus, the estimate was so high that the forest regeneration might be inhibited by deer herbivory in this forest.

But the vegetation structure (d.b.h. ≥ 5 cm) showed little change from 1990 to 2002 in the study area (Agetsuma *et al.* 2003), and no browse line was visible. In addition, a histogram of tree individual abundance (Fig. 1) did not show bell shape, compared with Kinkazan Island (Takatsuki & Gorai 1994). These facts indicate that the effect of deer herbivory had not emerged on the forest regeneration.

Exclosure efficiency

Fences prevent deer from browsing understory vegetation and disturbing the soil surface. In unfenced areas, deer can browse, stamp, and otherwise disturb seedlings and saplings and thus affect their growth and survival. Seedlings can vanish as a result of many factors, including soil erosion or disturbance, heavy rain, herbivory, or physical damages by fallen branches or animals. Herbivory and other activity of sika deer have no impact in a fenced exclosure.

Table 4. †Deer pellet counts

Date	Cumulative duration	No. pellets	No. pellets (estimated) Mean	Max.
2002/7/5–6	0			
2002/7/18	12.5	161	177.1	194.8
2002/7/31	25.5	352	388.6	429.1
2002/8/8	33.5	34	36.1	38.4
2002/8/17	42.5	51	54.6	58.5
2002/9/5	61.5	209	241.5	279.1
2002/9/19	75.5	355	394.9	439.4

†No. deer pellets were estimated by the pellet decay rate $c = 0.37 \pm 0.28$ pellets/month (mean ± SD, n = 22).

We observed differences in the degrees of seedling mortality and survival between fenced and unfenced quadrats. Differences in the composition of dead conditions were also observed. Deer effect on seedling establishment was not measured directly by the differences between the two treatments because various factors would cause seedling death. The death caused by deer herbivory or physical disturbance can be hidden among other mortality, especially for a low surviving species. In addition, sika deer effects can be over estimated because they can feed on artificially concentrated seedlings with ease.

Sika deer activity tended to decrease the current-year seedling mortality of small-seeded species but increased that of large-seeded species. When the relative mortality rate is high, the deer effects are also high. However, the low relative mortality rate does not mean that the deer effect is small. Deer effects are buried in other mortality. Thus, the relative mortality rate did not express sika deer effects on current-year seedling.

On the other hand, we used the relative survival rate to measure how many seedlings which should have survived without deer were reduced by sika deer activity. The relative survival rate was high for not-preferred species rather than preferred species, and small seeded species had high values in comparison with large seeded species which had low to high values. The composition of dead conditions for La, Ns, and So showed great difference between fenced and unfenced quadrats (Fig. 3). This was probably because the survivability had been greatly affected by deer herbivory for these preferred species.

We suggested that seedling survivability of not-preferred species was reduced only by physical damage of deer activity, while that of preferred species were reduced not only by physical damage but also by herbivory. Although Kobayashi & Kamitani (2000) suggested that minute-seeded species largely depend on the soil-surface disturbance for seedling emergence, we supposed that the physical disturbance could be an important mortality for both preferred and not-preferred species.

Feeding Pressure

Differences in feeding pressure on tree species can be explained by differences in feeding preferences of the herbivory (Takatsuki 1989; Du Toit *et al.* 1990), which can in turn, be determined by plants' defensive strategy. Anti-herbivory strategies are either 'exposing' strategies or defensive strategies, chemical or physical/mechanical defences (Takatsuki 1989).

But not all preferred species had a high increase of mortality. On the contrary, the relative mortality rate did not differ significantly between preferred species and not-preferred species, and the relative mortality rate had positive correlation to the seed weight (Fig. 4). As current-year seedling sizes are related to seed size (Fig. 6, Grime & Jeffrey 1965; Stock *et al.* 1990), this means that the feeding preference is less important for the increase of seedling mortality than the current-year seedling sizes. Seedlings can be chosen to be damaged according to their sizes rather than pre-existing feeding preferences.

Our results are similar to the result of Hoshizaki *et al.* (1997), who reported that the large seeds and seedlings of *Aesculus turbinate* (Hippocastanaceae) were more attractive to herbivores than smaller-seed species. As for seed size, larger seed size promotes seedling growth and survival (Schupp 1995) but incurs the risk of predation by rodents, which tend to prefer larger seeds (Westoby *et al.* 1992), while smaller seed size promotes effective seed dispersal (Schupp 1995) and can have greater probability of escape from predation (Schupp 1995). Besides, small seeded species also have a numerical advantage that they can yield many seeds (De Steven 1991).

Large seeded species had greatly influenced the increase of mortality, but did not influence the decrease of seedling survivability for not-preferred species, Sb. Thus, we supposed that the degree of the effect on seedling mortality and on survivability could be at variance with each other. and when the seedlings of small-seeded preferred species become large, these are probably herbivored and inhibited their establishment. The small seed size advantage would not last for a long time.

In this forest, seedling herbivory or physical disturbance by the high density of sika deer affected seedling mortality and survivability of preferred species as well as not-preferred species. Before monitoring and evaluating how seedlings and saplings actually survive and grow in this high sika deer density, we could not judge whether deer herbivory can cause severe damage on forest regeneration or not, although damage to vegetation in the study area does not seem apparent (Agetsuma *et al.* 2003). Agetsuma *et al.* (2003) suggested three factors which allow deer to persist at high density in the study area without causing severe damage to vegetation structure: (i) the smallest *C. n. yakushimae* size of all *C. nippon* subspecies; (ii) the high carrying capacity of evergreen forests, particularly in winter, and (iii) the coexistence of natural forest and native sika deer without predation and significant disturbances. We add another possible factor: (iv) the deer population density was increasing and we might have not found any sign of vegetation damages. In this case, the damage to vegetation structure could arise in the future.

The present study revealed that sika deer influenced the mortality and survivability of the current-year seedling. Because the damages caused by the high density of sika deer have a complex and lagged effect, we cannot predict that the forest will be maintained in this high deer density. To clarify this, we require further research such as long-term vegetation and deer population density dynamics, feeding activity of sika deer, long-term change of species composition between the inside and outside of exclosures.

Acknowledgements

We would like to thank my friends and colleagues in Yakushima for their hospitality and help during the field work. We are also grateful for Yakushima Forest Environment Conservation Center for giving us permission to undertake the research. Our thanks also to the Sarugoya Committee and Field Research Center of Primate Research Institute at Kyoto University who offered us excellent facilities, and to Dr N. Noma, Dr N. Agetsuma, Dr S. Aiba, and the members at the Center for Ecological Research, Kyoto University provided us with helpful suggestions and comments on the manuscript.

References

Agetsuma N., Sugiura H., Hill D. A., Agetsuma-Yanagihara Y. & Tanaka T. (2003) Population density and group composition of Japanese sika deer (*Cervus nippon yakushimae*) in an evergreen broad-leaved forest in Yakushima, southern Japan. *Ecological Research* **18**: 475–483.

Asada M. & Ochiai K. (1996) Food habitats of sika deer on the Boso Peninsula, central Japan. *Ecological Research* **11**: 89–95.

Bratton S. P. (1974) The effect of the European wild boar (*Sus scrofa*) on the high-elevation vernal flora in Great Smoky Mountains National Park. *Bulletin of the Torrey Botanical Club* **101**: 198–206.

De Steven D. (1991) Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* **73** (3): 1076–1088.

Du Toit J. T., Brayant J. P. & Frisby K. (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. *Ecology* **71** (1): 149–154.

Edwards G. R. & Crawley M. J. (1999) Rodent seed predation and seedling recruitment in mesic grassland. *Oecologia* **118**: 288–296.

Griffin J. R. (1971) Oak regeneration in the upper Carmel Valley, California. *Ecology* **52**: 862–868.

Grime J. P. & Jeffery D. W. (1965) Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* **53**: 621–642.

Hobbs N. T., Baker D. L., Ellis J. E. & Swift D. M. (1981) Composition and quality of elk winter diets in Colorado. *Journal of Wildlife Management* **45**: 156–171.

Hoshizaki K., Suzuki A. & Sasaki S. (1997) Impacts of secondary seed dispersal and herbivory on seedling survival in *Aesculus turbinate*. *Journal of Vegetation Science* **8**: 735–742.

Ickes K., Dewalt S. J. & Appanah S. (2001) Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. *Journal of Tropical Ecology* **17**: 191–206.

Ida H. & Nakagoshi N. (1996) Gnawing damage by rodents to the seedlings of Fagus crenata and *Quercus mongolica* var. *grosseserrata* in a temperate Sasa grassland-deciduous forest series in southwestern Japan. *Ecological Research* **11**: 97–103.

Iwamoto T., Sakata T., Nakazono T., Kaoka H., Ikeda K., Nishishita Y., Tokida K. & Doi T. (2000) Improvement of the pellet count method for the estimation of sika deer density. *Mammalian Science* **40** (1): 1–17 (In Japanese with English summary).

Kikuzawa K. (1988) Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest. *Forest Ecology and Management* **25**: 1–8.

Kobayashi M. & Kamitani T. (2000) Effects of surface disturbance and light level on seedling emergence in a Japanese secondary deciduous forest. *Journal of Vegetation Science* **11**: 93–100.

McCarthy B. C. & Facelli J. M. (1990) Microdisturbances in old-fields and forests: miplications for woody seedling establishment. *Oikos* **58**: 55–60.

McInnes P. F., Naiman R. J., Pastor J. & Cohen Y. (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* **73** (6): 2059–2075.

Myster R. W. & McCarthy B. C. (1989) Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. *Oikos* **56**: 145–148.

Nakashizuka T. (1988) Regeneration of beech (*Fagus crenata*) after the simultaneous death of underground dwarf bamboo (*Sasa kurilensis*). *Ecological Research* **3**: 21–35.

Noma N. (1997) Annual fluctuations of sapfruits production within and inter species in a warm Temperate forest on Yakushima Island. *Tropics* **6** (4): 441–449.

Ostfeld R. S. & Canham C. D. (1993) Effects of meadow vole population density on tree seedling survival in old fields. *Ecology* **74** (6): 1792–1801.

Pease J. L., Vowles R. W. & Keith L. B. (1979) Interaction of snowshoe hares and woody vegetation. *Journal of Wildlife Management* **43**: 43–60.

Schupp E. W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* **82** (3): 399–409.

Shaw M. W. (1968) Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in north Wales II. Acorn losses and germination under field condition. *Journal of Ecology* **56**: 647–660.

Sork V. L. (1987) Effeces of predation and light on seedling establishment in *Gustavia superba*. *Ecology* **68** (5): 1341–1350.

Stock W. D., Pate J. S. & Delfs J. (1990) Influence of seed size and quality on seedling development under low nutrient conditions in five Australian and South African members of the Proteaceae. *Journal of Ecology* **78**: 1005–1020.

Tagawa H. (1980) Vegetation on the western slope of Mt. Kuniwaridake, Yakushima Island. *Science Reports of Kagoshima University* **29**: 121–137 (In Japanese with English summary).

Takatsuki S. (1988) Rumen contents of sika deer on Tsushima Island, western Japan. *Ecological Research* **3**: 181–183.

Takatsuki S. (1989) Effect of deer on plants and plant communities. *Japanese Journal of Ecology* **39**: 67–80 (In Japanese with English summary).

Takatsuki S. (1990) Summer dietary compositions of sake deer on Yakushima Island southern Japan. *Ecological Research* **5**: 253–260.

Takatsuki S. & Gorai T. (1994) Effects of Sika deer on the regeneration of a Fagus crenata forest on Kinkazan Island, northern Japan. *Ecological Research* **9**: 115–120.

Takatsuki S., Kanomata K. & Suzuki K. (1981) Defecation rates of Sika deer and Japanese serow. *Japanese Journal of Ecology* **31**: 435–439 (In Japanese with English summary).

Tardiff S. E. & Stanford J. A. (1998) Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. *Ecology* **79** (7): 2219–2228.

Weltzin J. F., Archer S. & Heitschmidt R. K. (1997) Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* **78** (3): 751–763.

Westoby M., Jurado E. & Leishman M. (1992) Comparative evolution ecology of seed size. *Trends in Ecology and Evolution* **7**: 368–372.

Wilby A. & Brown V. K. (2001) Herbivory, litter and soil disturbance as determinants of vegetation dynamics during early old-field succession under set-aside. *Oecologia* **127**: 259–265.

Yokoyama M., Kaji K. & Suzuki M. (2000) Food habitats of sika deer and nutritional value of sika deer diets in eastern Hokkaido, Japan. *Ecological Research* **15**: 345–355.