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Determinant factors in the seedling establishment of *Pasania edulis* (Makino) Makino

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Abstract *Pasania edulis* (Makino) Makino is one of the dominant *Fagucea* tree species in evergreen broad-leaved forests in southern Japan, and its regeneration success may have a major impact on the dynamics of evergreen broad-leaved forests. We conducted a field survey on the population process from acorn production to seedling establishment of *P. edulis* in an evergreen broad-leaved forest in Kagoshima, southern Japan, from 1995 to 2009. The acorn crop varied greatly among the 14 cohorts, with mast cropping being recorded every 3–4 years. The mortality rate of acorns was very high for all 14 cohorts (99.3–100 %). Important mortality factors were failure to mature (empty acorns), attack by *Curculio* weevil on trees, predation of dropped acorns by *Apodemus* mice and large or medium-sized mammals (wild boar (*Sus scrofa leucomystax*), badger (*Meles meles anakuma*), and raccoon dog (*Nyctereutes procyonoides viverrinu*)), and attacks on germinated acorns by the acorn borer (*Coccotrypes graniceps*). Among these factors, predation by *Apodemus* mice was the greatest contributor to annual fluctuations in total mortality until seedling establishment. Large or medium-sized mammals and the acorn borer also caused severe damage to dropped acorns in some years, but contributed little to annual fluctuations in total mortality. For successful regeneration, mast cropping was essential. However, a small population of *Apodemus* mice, that is, a low predation pressure, was also required during mast years.

Keywords *Apodemus* mice · Life table analysis · Mastling · *Pasania edulis* · Population process · Seedling establishment

Introduction

Tree species produce and disperse seeds to regenerate and expand their distributed area. However, seeds are also a food resource for many granivorous and omnivorous animals. Many seeds produced by trees do not establish as seedlings, because they are subject to mortality from a range of sources, namely, predation by mammals and insects on the tree (e.g., Tanaka et al. 1989; Maeto 1995; Sone et al. 2002), predation by mammals after dropping to the ground (e.g., Shaw 1968; Watts 1968; Zemanek 1972; Sato 2000; Shimada 2001; Sone et al. 2002), and attacks on germinated acorns by mammals, insects, and microbes (e.g., Ueda et al. 1993; Sone et al. 2002). Therefore, seed predation and other forms of seed mortality during the early stages of the population process (i.e., the period from seed production to seedling establishment) may have a serious impact on the regeneration of tree species.

Some rodents are known to hoard surplus foods when they are temporarily supplied with abundant food, and are thought to contribute to seed dispersion and the regeneration of trees through hoarding activities (e.g., West 1968; Smith and Reichman 1984; Jensen and Nielsen 1986; Miyaki and Kikuzawa 1988; Vander Wall 1990; Tamura 2001; Takahashi et al. 2006). Because many rodents are nocturnal, it is very difficult to observe their hoarding behavior directly in the field. To date, many studies have been conducted on census methods for the hoarding behavior of rodents (e.g., Yasuda et al. 1991; Tamura 1994; Isaji and Sugita 1997; Sone and Kohno 1996; Xiao et al. 2006; Yi et al. 2008), and the processes causing the disappearance of dropped or artificially located/buried acorns have been traced using various methods to elucidate the role of these animals on seed dispersion and seedling establishment (e.g., Sone

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and Kohno 1996, 1999; Akashi 1997; Iida 2006; Takahashi et al. 2006; Xiao et al. 2006; Hirata et al. 2007; Yamagawa et al. 2010). However, most of these studies were conducted over a short period of 1–3 years.

The seed production of tree species belonging to *Fagucea* varies greatly from year to year, with cyclic mast cropping occurring at 3- to 7-year intervals (e.g., Kanazawa 1982; Kohyama 1982; Hashizume 1987; Imada et al. 1990; Takeda 1992; Harmer 1994). Therefore, long-term studies covering at least 2 or more cycles (i.e., 10–15 years) of fluctuations in seed production are required to identify the conditions needed for the successful regeneration of acorn-producing tree species, and to evaluate the role of the hoarding animals in the process of regeneration.

Pasania edulis (Makino) Makino (*Fagucea*) is a dominant tree species in many evergreen broad-leaved forests of southern Japan, in which two species of granivorous mice, namely, *Apodemus speciosus* Temminck and *A. argenteus* Temminck (Rodentia: Muridae), are distributed widely (Imaizumi 1960; Doi and Iwamoto 1982). *P. edulis* trees show major year-to-year variation in acorn production (Sone et al. 2002). Because of their large size (2–4 g: 5–10 cal acorn⁻¹) and low tannin content (0.5 %), *P. edulis* acorns are the primary food resource of *Apodemus* mice during autumn and winter. In addition to *Apodemus* mice, the giant flying squirrel (*Petaurista leucogenys*) and *Curculio* weevils attack acorns on trees. Furthermore, dropped acorns are fed on by large or medium-sized omnivorous mammals such as wild boar (*Sus scrofa leucomystax*), badger (*Meles meles anakuma*), and raccoon dog (*Nyctereutes procyonoides viverrinus*), as well as the acorn borer (*Coccotrypes graniceps*) until seedling establishment (Sone et al. 2002). Among these predators, the two species of *Apodemus* mice not only feed on but also hoard acorns of *P. edulis* less than 5 cm in the soil (Sone and Kohno 1996, 1999; Sone et al. 2002), and their hoarding activity facilitates germination if not recovered or pilfered as Vander Wall (1990) pointed out. Consequently, it is possible that these mice not only interfere with but also facilitate the regeneration of *P. edulis* trees.

Sone et al. (2002) speculated on the conditions required for the regeneration of *P. edulis* and the role of *Apodemus* mice during the early stages of its population process. This work was accomplished through the life table analysis, using the data of *P. edulis* acorn crops from five cohorts, in parallel to a survey of the hoarding behavior of *Apodemus* mice. However, the five cohorts represent just one cycle in the fluctuation of acorn production. Hence, we continued the field studies, and calculated the life tables for 14 cohorts of acorns produced from 1995 to 2008, covering three cycles in the fluctuation of acorn production. In this paper, we describe the results of the life table analysis for the 14 cohorts of *P. edulis* acorns, and discuss the conditions and determinant factors required for successful regeneration of *P. edulis* and the role of *Apodemus* mice in this process.

Methods

Study site

This study was conducted at the Takakuma Experimental Forest of Kagoshima University (31°31'N, 130°46'E, and 550 m in altitude) in Kagoshima prefecture, southern Japan. Annual mean temperature and precipitation during the last decade were 14.3 °C and 3,460 mm, respectively. In May 1994, we established a study site of approximately 2 ha in size that was situated on a wide ridge, adjoining a north-facing slope in a secondary evergreen broad-leaved forest. The crown layer of the stand was closed, and *P. edulis* was the most dominant species and occupied about 50 % of canopy trees. Other dominant tree species were *Castanopsis cuspidata*, *Machilus thunbergii*, *Neolitsea sericea*, *Distylium racemosum*, *Quercus acuta*, and *Quercus salicina*. The understory vegetation was composed of *Cleyera japonica*, *Symplocos lucida*, *Camellia japonica*, and *Illicium anisatum*. A plantation of the Japanese cedar, *Cryptomeria japonica*, was situated to the south of the study site.

Aside from *P. edulis* acorns, some acorns of *C. cuspidata* and the seeds of *Acer rufinerve* and *Cornus kousa* dropped into seed traps almost every year. Although the acorns and seeds of these tree species are available as foods for granivorous mammals, they are much smaller and less abundant than *P. edulis* acorns (K.S., unpublished data). These findings suggest that at the study site, acorn crops of *P. edulis* are the most important food resource and primarily determine food conditions for granivorous mammals during autumn and winter.

At the study site, besides the two species of *Apodemus* mice, handling of acorns by *M. meles*, *S. scrofa leucomystax*, and *N. procyonoides albus* was photo-trapped frequently (K.S., personal observations). The feeding scar of *P. leucogenys* was recorded in a few occasions (Sone et al. 2002). The Japanese monkey (*Macaca fuscata*), the Japanese squirrel (*Sciurus lis*), and Sika deer (*Cervus nippon nippon*) also eats acorns, but we did not observe them during the study period. The Eurasian Jay (*Garrulus glandarius*) and the large-billed crow (*Corvus macrorhynchos*) can handle acorns, but their acorn handling on the ground was photo-trapped on only few occasions. Therefore, the two species of *Apodemus* mice and large or medium-sized mammals were thought to be the most important predatory vertebrates for *P. edulis* acorns.

Mice populations

We set up a study plot measuring 65 × 55 m in the central part of the study site, where we established 56 trap stations at approximately 7-m intervals in a grid (8 rows × 7 columns). We conducted four or five successive night censuses in November 1995, and every month from July 1996 to May 2009. However, we stopped the census from mid-December to mid-March because 10–30 % of

captured mice died due to a spell of cold weather on preliminary census occasions. We set a cage trap ($9 \times 10 \times 17$ cm) to catch mice with raw peanuts and sunflower seeds as bait and leaf litter and pieces of corrugated cardboard for protection of the captured mice against the cold at each trap station. Each trap was covered with a nylon sheet to prevent the captured mouse from being drenched. We checked the traps every morning. We identified each captured mouse by toe clipping at its first capture, and recorded the trap station where the mouse was captured, species, individual number, and various other characteristics. We then released the mouse at the trap station of capture. The captured mice were divided into two groups: (1) mice actively foraged on the study plot during the census period (the resident mice), and (2) mice captured occasionally. In this study, we defined resident mice in autumn and winter as those that were (1) captured regularly on more than half of census occasions during the acorn-dropping season and (2) captured both in the November/December and March/April censuses. During the 1995–1996 season, we could conduct the census only in November 1995 and July 1996. Therefore, we defined the mice captured on both census occasions as residents.

Acorn crop

We set 24 seed traps (50×50 cm) at 1 m height above the ground at 10–20 m intervals throughout the study plot in mid-September 1995. Each trap was supported with three wooden stakes that allowed the mice to access the trap. We counted the number of acorns dropped into each trap every week from early September to late November. On each census occasion, we marked newly dropped acorns with ink, and counted the number of acorns that had been marked to check for the foraging of acorns in traps or the carriage of acorns from traps by mice. Ink marking did not interfere with either consumption or transportation of the acorns by *Apodemus* mice (Sone and Kohno 1996, 1999). At the end of October of each year, when most acorns had dropped, we randomly collected 1,000–8,000 acorns from the ground. We categorized the collected acorns into 4 groups as follows; sound, abortion (failure to mature), foraged by mammals (mainly *P. leucogenys*) on the trees, and ingested by insects (mainly *Curculio* weevils), and counted the number of acorns within each group to estimate the mortality rate of acorns on trees due to each factor.

Transportation and predation of dropped acorns

We established four plots measuring 1×1 m in the northeastern, central, and southwestern parts of the study plot, respectively, in September 1995. We

numbered newly dropped acorns with ink, and checked the presence or absence of each numbered acorn in each plot at approximately 1-week intervals until all sound acorns had disappeared. When the acorns were eaten on the plot, we recorded the acorn number on the remains of the nutshell and attempted to identify the predator species by using the teeth marks on the nutshells and photo-traps by a camera with an infrared sensor switch (Fieldnote II, Marifu, Iwakuni, Japan). Based on this information, we estimated the ratio of dropped acorns predated by *Apodemus* mice and large or medium-sized mammals on the plots and those transported by *Apodemus* mice from the plots.

To estimate the ratio of acorns that were hoarded after being transported by *Apodemus* mice, we established a food station in the same three areas in September 1995. Each food station was covered with an 8 mm wire mesh cage ($30 \times 30 \times 20$ cm) that was lifted 5 cm above the ground, to allow only *Apodemus* mice access to the acorns in the food station. To trace the fate of the acorns transported by *Apodemus* mice, we tagged miniature transmitters ($9 \times 7 \times 20$ mm; antenna length, 11 cm; weight, 2.1 g; model 393 or F515, ATS, Isanti, MN) on the seed coat of each acorn with a water-proof bond (Konishi, Tokyo, Japan) (T-acorns). The weight of the T-acorns ranged from 5.0 to 7.0 g. Sone and Kohno (1996) reported that the attachment of a transmitter to a *P. edulis* acorn did not interfere with the hoarding activity of *A. speciosus*. We placed two or three T-acorns together with 10–50 *P. edulis* acorns that were marked with ink at each of the 3 food stations. At 1–7 days later, we located the position of each T-acorn using a receiver (FT-690mk II, Vertex Standard, Tokyo, Japan) and recorded the condition of the acorn (eaten or hoarded). We traced the fate of 16–57 T-acorns each year.

Fate of hoarded acorns

Besides the trace of the fate of each T-acorn, we buried acorns artificially in the soil at the end of the acorn-dropping season (i.e., from late-October to late-November) every year from 1996 to 2008. At our study site, mice either hoarded single acorns in the soil just beneath the litter layer (scatter hoarding) or hoarded four or five acorns in the soil at 10–15 cm depth (larder hoarding) (K.S., unpublished data). Therefore, we selected 24 undergrowth trees in 1996, 40 trees in 1997 and 1998, 53 trees in 1999, and 55 trees in 2000–2008 for scatter and larder hoarding plots. We marked selected trees with colored tape at about 1.5 m height above the ground. The trees were distributed uniformly at approximately 7–10 m intervals at and near the study plot. For scatter hoarding, we cached a single acorn ≤ 5 cm deep in the soil at four hoarding sites located on the circumference of a circle, with a radius of 20 cm at 90° directional intervals around each selected tree. For larder hoarding, we buried five acorns 10–15 cm deep in

the soil at a site located 20 cm from the trunk of the selected tree. We checked the survival of each acorn in each cache at 1–4 month intervals. If the cache site was dug up and vertical hole measuring greater than 10 cm in diameter remained, we considered the acorn(s) to be consumed by large or medium-sized mammals. If there was a horizontal or vertical tunnel measuring 3–4 cm in diameter at the hoarding site, we considered the acorn(s) to have been removed by *Apodemus* mice.

Data analysis

Based on data on acorn crops and acorn mortality due to each factor at each stage estimated by the methods of Sone et al. (2002), we calculated life tables for 14 cohorts of *P. edulis* acorns that were produced from 1995 to 2008.

To determine the mortality factor that contributed the most to the annual fluctuation in the total mortality from acorn production on the trees to seedling establishment (Total K), the “key factor”, we divided Total K into three stage mortalities as follows:

k_1 : Mortality on trees. k_1 was further divided into three submortalities; the failure to mature (empty acorns) (k_{11}), the mortality due to the attack by *Curculio* weevils (k_{12}), and that due to the predation by mammals (mainly *P. leucogenys*) (k_{13}).

k_2 : Mortality from dropping to germination. k_2 included mortalities due to the predation by *Apodemus* mice (k_{21}), that by large or medium-sized animals (*S. scrofa leucomystax*, *M. meles*, and *N. procyonoides albus*) (k_{22}), and rotting and/or other factors (k_{23}).

k_3 : Mortality from germination to seedling establishment. k_3 included mortalities due to the predation by *Apodemus* mice (k_{31}), that by large or medium-sized mammals (k_{32}), the attack by the acorn borer (k_{33}), and unknown factors (k_{34}).

K -, k_i -, and k_{ij} -values were calculated as follows (Varley and Gradwell 1960):

$K = \log(\text{no. of produced acorns on trees}) - \log(\text{no. of seedlings established in the first season})$

$k_i = \log(\text{no. of acorns at the beginning of stage } i) - \log(\text{no. of acorns at the beginning of stage } i + 1)$,

$k_{ij} = \log(\text{no. of acorns before the mortality factor } j \text{ acted during the stage } i) - \log(\text{no. of acorns after the mortality factor } j \text{ acted during the stage } i) = -\log(1/q_{ij})$

where q_{ij} is the mortality rate due to the mortality factor j during the stage i , $K = k_1 + k_2 + k_3$, $k_1 = k_{11} + k_{12} + k_{13}$, $k_2 = k_{21} + k_{22} + k_{23}$, and $k_3 = k_{31} + k_{32} + k_{33} + k_{34}$.

During each stage of the population process, two or more mortality factors acted on acorns. In this study, we estimated the mortality rate due to each factor assuming that they acted simultaneously on the acorns.

In life table data analysis, we identified a key factor using the regression method presented by Podoler and Rogers (1975). In this method, k_i - and k_{ij} -values are plotted on the y -axis against K - and k_i -values on the x -axis, respectively, and the mortality that provides the highest regression coefficient is designated as the key factor. The density relationship of each mortality was examined by calculating the correlation coefficient between K -, k_i -, and k_{ij} -value and the log-transformed acorn density.

Results

Annual changes in acorn crops of *Pasania edulis*

The number of acorns produced on trees varied greatly from 38,000 to 692,000 acorns ha^{-1} (Fig. 1). In this study, we tentatively classified acorn production into four classes as follows: mast ($>400,000$ acorns ha^{-1} were produced), semi-mast (about 300,000 acorns ha^{-1}), medium (100,000–300,000 acorns ha^{-1}), and poor ($<100,000$ acorns ha^{-1}). According to this criterion, mast cropping was recorded in 4 years (1996, 1999, 2003, 2006), semi-mast cropping in 2002 and 2007, medium cropping in 4 years (1995, 1997, 2000, 2001), and poor cropping in 4 years (1998, 2004, 2005, 2008).

Annual changes in the number of resident mice

Two granivorous *Apodemus* mice, *A. speciosus* and *A. argenteus*, were captured on each census occasion. Two species of rodents (*Microtus montebelli* and *Urotrichus talpoides*) were caught on a few occasions.

The number of resident *A. speciosus* and *A. argenteus* mice during autumn and winter ranged from 1 to 16.5 and from 1 to 13.5 individuals, respectively (Fig. 1). The numbers of resident individuals of both species were

Fig. 1 Annual changes in the numbers of resident *Apodemus* mice during autumn and winter (left y -axis) and dropped acorns (bars) (right y -axis)

highest during the 1996–1997 season, and showed a similar pattern in annual fluctuation. The total number of resident mice ranged from 2 to 30 individuals. If we tentatively classified the abundance of resident mice as follows; abundant (> 15 mice), intermediate (6–15 mice), and low (< 6 mice); the abundance of resident mice were categorized as abundant in the 1996–1997, 1997–1998, and 2007–2008 seasons, medium in the 1998–1999, 2000–2001, 2001–2002, and 2002–2003 seasons, and low in the 1995–1996, 1999–2000, 2003–2004, 2004–2005, and 2005–2006 seasons. Annual changes in the number of resident mice were not synchronized with the acorn crops (Fig. 1). In the past years, the number of resident mice was not categorized as abundant, except for the 1996–1997 seasons. In years with a poor acorn crop, the number of resident mice was low, except for the 2008–2009 season. In years with a medium acorn crop, the number of resident mice varied with the years.

Mortalities from acorn production on trees to seedling establishment

Table 1 shows the life tables of the 14 cohorts of *P. edulis* acorns produced on trees from 1995 to 2008 until they were established as seedlings in the following year. In the subsequent sections, we present a detailed description of the mortality at each stage.

Mortality on trees (k_1)

The mortality rate at this stage varied from 19.1 to 52.4 %. The primary mortality factor was abortion (failure to mature), which varied from 11.3 to 47.6 %. The other important mortality factor was predation by *Curculio* weevil larvae, and the predation rate varied from 4.8 to 23.8 %. The mortality rate due to other mortality factors such as predation by *P. leucogenys* was very low (0–2.1 %).

Mortality of dropped acorns until germination (k_2)

No or few acorns that dropped into the seed traps were predated or transported by animals. During the study period, 12,000–443,000 sound acorns ha^{-1} dropped to the ground. In total, *Apodemus* mice and large or medium-sized mammals predated 31.0–99.6 % of the acorns on the places where they dropped without being transported and hoarded by *Apodemus* mice. The predation rates by *Apodemus* mice and large or medium-sized mammals were subject to large variation among 14 cohorts, 0.8 to 99.6 % and 0 to 67.7 %, respectively.

The mortality rates of hoarded acorns were very high, i.e., 76.5–100 %. Predation by *Apodemus* mice and large or medium-sized mammals represented almost all of the

mortality of hoarded acorns. Rotting and other factors also destroyed 0.04–2.7 % of hoarded acorns.

As a result, 97.6–100 % of the acorns were predated by these mammals before they germinated. Predation rates by *Apodemus* mice and large or medium-sized mammals during this stage ranged from 20.0 to 100 % and 0 to 78.4 %, respectively. The predation rate by large or medium-sized mammals was zero or very low (< 3 %) in 3 of the 14 cohorts (cohort 1995, 2005, 2006).

Mortality of germinated acorns until seedling establishment (k_3)

The number of germinated acorns varied from 0 to 18,000 acorns ha^{-1} . The mortality rate of germinated acorns ranged from 12.5 to 100 %. The primary mortality factor was predation by *Apodemus* mice, which accounted for 16.7–100 % of mortality. The other important mortality factor was the attack by the acorn borer, which destroyed 0–66.7 % of the germinated acorns. Predation by large or medium-sized mammals and unknown mortality factors contributed little to the mortality of germinated acorns (0 % for 8 and 9 out of 12 cohort, respectively).

As a result, 0 to 3,413 acorns ha^{-1} were established as seedlings during the study period. Of the 14 cohorts, 5 (cohort 1995, 1997, 1998, 2004, 2005) did not produce any seedlings, and 3 (cohort 2000, 2001, 2008) produced few seedlings (< 100 seedlings ha^{-1}) in the first growing season. In contrast, about 1,000 or more seedlings ha^{-1} were established from the cohorts of mast (cohort 1996, 1999, 2003, 2006) or semi-mast years (cohort 2007) in the first growing season.

Life table analysis

Among the stage mortalities, the mortality of dropped acorns before germination (k_2) showed the highest regression coefficient (0.9006) to Total K (Table 2). Among the submortalities of k_2 , predation of dropped acorns by *Apodemus* mice (k_{21}) and that by large or medium-sized mammals (k_{22}) fluctuated compensatory to each other (Fig. 2). The regression coefficient of k_{21} on k_2 (0.7535) was much higher than that of k_{22} (0.0627), suggesting that k_{21} contributed most and k_{22} did not contribute to the annual fluctuations of k_2 (Table 3). Among the mortality factors, the regression coefficient on Total K was highest for k_{21} (0.6450) (Table 3). These results indicated that the predation of dropped acorns by *Apodemus* mice before germination (k_{21}) was the key factor causing the annual fluctuations of Total K .

Table 4 shows the density relationship of the total mortality (Total K), stage mortalities (k_i), and mortalities due to main factors (k_{ij}). A negative correlation with acorn density was detected by Total K , k_1 , k_2 , and k_{11} . k_{21} tended to act inversely with acorn density. A sig-

Table 1 Life tables for *Pasania edulis* acorns of 14 cohorts produced from 1995 to 2008

Stage (x)	Mortality factors (F)	Cohort 1995		Cohort 1996		Cohort 1997		Cohort 1998		Cohort 1999		Cohort 2000		Cohort 2001	
		No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)
Produced on trees	Failure to mature (abortion)	150,000	36.5 ^a 28.8	692,000	36.0 ^a 20.9	188,000	36.1 ^a 19.7	91,000	31.2 ^a 25.9	490,000	27.9 ^a 18.0	107,000	19.1 ^a 10.7	190,000	35.1 ^a 11.3
	Predation by weevil larvae		5.6		15.1		16.2		5.3		9.6		8.2		23.8
	Predation by mammals		2.1				0.2				0.3		0.2		
Dropped to the ground	Predation by <i>Apodemus</i> mice	95,250	31.0 ^a 31.0	442,880	91.4 ^a 48.8	120,132	54.3 ^a 27.9	62,608	32.6 ^a	353,290	46.2 ^a 10.9	86,563	21.8 ^a 0.8	123,310	64.3 ^a 17.9
	Predation by large and medium-sized mammals				42.6		26.4		32.6		35.3		21.0		39.3
	Others, unknown														
Transported and hoarded by <i>Apodemus</i> mice	Predation by <i>Apodemus</i> mice	65,722	100 ^a 100	38,088	95.3 ^a 71.2	54,900	99.8 ^a 85.5	42,198	100 ^a 41.3	190,070	90.5 ^a 56.5	67,692	95.6 ^a 54.1	44,022	95.5 ^a 44.7
	Predation by large and medium-sized mammals				23.3		13.9		58.1		31.3		41.5		50.8
	Rotting, others														
Germinated	Predation by <i>Apodemus</i> mice				0.8		0.4		0.6		2.7		7.0		66.7
	Predation by large and medium-sized mammals				50.0 ^a		100		0		81.1 ^a 30.4		98.2 ^a 52.6		22.3
	Predation by the acorn borer						100								
Seedlings	Others, unknown				50.0						50.7		38.6		4.5
		0		895				0		3,413		54		129	

Table 1 continued

Stage (x)	Mortality factors (F)	Cohort 2002		Cohort 2003		Cohort 2004		Cohort 2005		Cohort 2006		Cohort 2007		Cohort 2008	
		No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)	No. of acorns	Mortality rate (%)
Produced on trees	Failure to mature (abortion)	307,000	23.1 ^a 13.6	500,000	22.7 ^a 16.0	47,000	52.4 ^a 47.6	38,000	47.1 ^a 30.0	488,000	27.5 ^a 16.0	318,000	30.3 ^a 17.0	75,000	40.0 ^a 23.7
	Predation by weevil larvae		9.5		6.4		4.8		17.1		11.5		13.3		16.3
	Predation by mammals	236,083	68.9 ^a	386,500	64.5 ^a	22,372	86.4 ^a	20,102	99.6 ^a	353,800	69.9 ^a	221,646	89.7 ^a	45,000	71.5 ^a
Dropped to the ground	Predation by <i>Apodemus</i> mice		1.2		1.2		79.7		99.6		66.7		49.9		44.7
	Predation by large and medium-sized mammals		67.7		62.5		6.7				3.2		39.8		26.8
	Others, unknown				0.8										
Transported and hoarded by <i>Apodemus</i> mice	Predation by <i>Apodemus</i> mice	73,422	96.2 ^a 71.6	137,207	97.8 ^a 53.0	3,043	99.7 ^a 97.9	80	97.4 ^a 97.4	106,494	97.8 ^a 97.8	22,830	76.5 62.6	12,825	93.1 ^a 92.3
	Predation by large and medium-sized mammals		24.6		44.8		1.6						13.6		0.8
	Rotting, others														
Germinated	Predation by <i>Apodemus</i> mice	2,790	92.8 ^a	3,019	12.5 ^a		0.2 33.3	2	100 ^a 92.9	23,423	58.3 ^a 16.7	5,365	59.6 ^a 51.5	885	83.3 ^a
	Predation by large and medium-sized mammals										8.3		2.0		0.04
	Predation by the acorn borer		92.8		12.5		66.7	7.1			33.3		4.1		
Seedlings	Others, unknown												2.0		83.3
		201		2,641		0		0		977		2,168		148	

^a Total mortality at each stage

nificant density relationship was not detected in k_{22} , k_3 and its submortalities (k_{3j}).

Discussion

Mast cropping has been recorded by many tree species of *Fagaceae* (e.g., Kanazawa 1982; Kohyama 1982; Hashizume 1987; Imada et al. 1990; Takeda 1992; Harmer 1994). During the study period, the acorn production of *P. edulis* also varied greatly, and mast cropping was recorded at 3- or 4-year intervals. Abundance of seed production has great impacts on the regeneration of acorn-producing tree species and some pine species (e.g., Imada et al. 1990; Vander Wall 2002; Jansen et al. 2004; Sun et al. 2004; Garcia et al. 2005). Therefore, mast cropping might have considerable impact on the regeneration of *P. edulis* at the study site.

Acorns are subject to mortality caused by various factors from production on trees to seedling establishment. In this study, the mortality rate of acorns produced on trees before seedling establishment was very high, i.e., 99.7–100 %, for all 14 cohorts. The mortality rate was higher for dropped acorns than acorns on trees. A high mortality rate of dropped acorns was also reported for other *Fagaceae* tree species (e.g., Kanazawa 1982; Yamashita 1994; Akashi 1997).

The main mortality factors were the attack by *Curculio* weevil on trees, the predation by *Apodemus* mice and large or medium-sized mammals from dropping to germination, and the attack by the acorn borer from germination to seedling establishment. Among these four mortality factors, predation by *Apodemus* mice (k_{21}) caused the highest rate of mortality and was thought to have the greatest impact on the population process of *P. edulis* as reported for other acorn-producing tree species by Shaw (1968), Watts (1968), Zemanek (1972), Sato (2000), Shimada (2001), and others. Large or medium-sized mammals (k_{22}) were also responsible for the mortality of dropped acorns in some cohorts. Predation by these two groups of mammals showed compensatory fluctuation, indicating that these two groups competed for dropped acorns at the study site.

The analysis of life table data showed that the annual fluctuation pattern in the total mortality (Total K) was determined mainly by that of mortality due to the predation by *Apodemus* mice (k_{21}) and that the annual fluctuation of the predation of dropped acorns by the *Apodemus* mice should be a determinant factor of that of seedling establishment for *P. edulis* as Sone et al. (2002) had speculated. The tendency of k_{21} to act in a negative density relationship suggests that more acorns could escape from predation by *Apodemus* mice and establish as seedlings in mast years. *Curculio* weevils, large or medium-sized mammals, and the acorn borer were responsible for the high mortality of acorns on trees, dropped acorns, and germinated acorns, respectively, in some years. However, these mortality factors acted on acorns in a density-independent manner. Therefore, although the predation by these animals occasionally led a high mortality of acorns, it was not a determinant factor in the annual fluctuation pattern of seedling establishment. The failure of acorns to mature (k_{11}) also correlated negatively with the number of acorns produced on trees, as reported by Tanaka et al. (1989). However, the regression coefficient of k_{11} to Total K was much lower than that of k_{21} ; k_{11} seemed to contribute little to the annual fluctuations in the total mortality and seedling establishment.

Table 2 Regression coefficients (r) for various k_i - and k_{ij} -values on Total K

k values	Regression coefficients
k_1	0.0309
k_2	0.9006
k_3	0.0837
k_{11}	0.0309
k_{12}	-0.0009
k_{13}	0.0009
k_{21}	0.6450
k_{22}	0.2584
k_{23}	-0.0022
k_{31}	0.1828
k_{32}	-0.0121
k_{33}	-0.0684
k_{34}	-0.0376

Fig. 2 Annual changes in the mortality of dropped acorns due to predation by *Apodemus* mice (k_{21}) and that due to predation by large or medium-sized animals (k_{22})

Table 3 Regression coefficients for various k_{2j} -values on k_2

k_{2j} values	Regression coefficients
k_{21}	0.7535
k_{22}	0.0627
k_{23}	-0.0021

Table 4 Correlation coefficients (r) for mortality and main mortality factors on the density of *P. edulis* acorns

Mortality/mortality factors	r	P
Total mortality of acorns (Total K)	-0.675	**
Mortality of acorns on the tree (k_1)	-0.662	**
Empty (k_{11})	-0.630	*
Attacked by weevil larvae (k_{12})	-0.065	ns
Mortality of acorns during dropping and germinating (k_2)	-0.573	*
Predating by <i>Apodemus</i> mice (k_{21})	-0.512	ms
Predating by large or medium-sized mammals (k_{22})	0.037	ns
Mortality of acorns after germinating (k_3)	-0.053	ns
Predation by <i>Apodemus</i> mice (k_{31})	-0.194	ns
Predation by large or medium-sized mammals (k_{32})	0.068	ns
Attacked by the acorn borers (k_{33})	0.154	ns

* Correlation significant at $P = 0.05$ level, ** correlation significant at $P = 0.01$ level, *ms* correlation significant at $P = 0.1$ level, *ns* correlation insignificant at $P = 0.1$ level

Table 5 presents a summary of the acorn crop, the abundance of resident *Apodemus* mice during autumn and winter, and the probability of seedling establishment in the first growing season for the 14 cohorts of *P. edulis* acorns. A high probability of regeneration success, seedling establishment, was expected for the cohort 1999, 2003, and 2007. In these cases, acorn production was categorized as mast or semi-mast. Cohorts of poor and medium crop years produced few seedlings. These

results show that mast cropping of acorns is necessary to produce a sufficient number of seedlings. A negative density relationship of Total K suggests that the more acorns produced, the more seedlings established. A large number of seedlings established in the season following mast years. This phenomenon has also been reported for other tree species (e.g., Imada et al. 1990; Vander Wall 2002; Jansen et al. 2004; Sun et al. 2004; Garcia et al. 2005).

However, mast cropping did not guarantee the production of plenty of seedlings alone. A small population of *Apodemus* mice might be needed. Although the most abundant acorns (692,000 acorns ha^{-1}) were produced in 1996, only 891 seedlings ha^{-1} were established in the first growing season and the probability of regeneration success was not expected to be high. In the autumn and winter of 1996/1997, the number of resident *Apodemus* mice was highest during the study period, and contributed to the high mortality of dropped acorns. For the successful regeneration of *P. edulis*, the control of predation pressure of *Apodemus* mice is also needed (Harmer 1994).

From these results, we conclude that, at this study site, mast cropping was a requisite but a small population of *Apodemus* mice, namely a low predation pressure was also necessary for the successful regeneration of *P. edulis*. At this study site, *Apodemus* mice reproduce only once a year from late autumn to early spring (Oishi et al. 2010), and the mice population could not increase immediately in the mast years as reported by Miguchi (1988) and Saitoh et al. (2008). This delayed increase in *Apodemus* mice population after mast cropping could produce a condition in which *Apodemus* mice acted as a seed disperser; mast cropping and a small population of *Apodemus* mice. For the acorn cohorts of years with poor and medium crop, *Apodemus* mice contributed little to regeneration of *P. edulis* trees irrespective of their population size, and acted as seed predators.

Table 5 Summary of acorn production, abundance of resident mice, and probability of regeneration for the 14 cohorts of *Pasania edulis* acorns produced during the period from 1995 to 2008

	Cohort 1995	Cohort 1996	Cohort 1997	Cohort 1998	Cohort 1999	Cohort 2000	Cohort 2001
Acorn crop	Medium	Mast	Medium	Poor	Mast	Medium	Medium
Abundance of resident mice	Low	Abundant	Abundant	Medium	Low	Low	Medium
Probability of seedling establishment ^a	×	○	×	×	⊙	△	△
	Cohort 2002	Cohort 2003	Cohort 2004	Cohort 2005	Cohort 2006	Cohort 2007	Cohort 2008
Acorn crop	Semi-mast	Mast	Poor	Poor	Mast	Semi-mast	Poor
Abundance of resident mice	Medium	Low	Low	Low	Medium	Medium	Abundant
Probability of seedling establishment ^a	△	⊙	×	×	○	⊙	△

^a×, probability is 0; △, probability is extremely low; ○, probability is rather high; ⊙, probability is high

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References

- Akashi N (1997) Dispersal pattern and mortality of seeds and seedlings of *Fagus crenata* Blume in a cool temperate forest in western Japan. *Ecol Res* 12:159–165
- Doi T, Iwamoto T (1982) Local distribution of two species of *Apodemus* mice in Kyushu. *Res Popul Ecol* 24:102–111
- Garcia D, Obeso JR, Martinez I (2005) Rodent seed predation promotes differential recruitment among bird-dispersed trees in temperate secondary forest. *Oecologia* 144:435–446
- Harmer R (1994) Natural regeneration of broadleaved trees in Britain: II Seed production and predation. *Forestry* 67:275–286
- Hashizume H (1987) Seed production in the secondary stand of Konara (*Quercus serrata* THUNB.) (in Japanese with English summary). *Hardwood Res* 4:19–27
- Hirata R, Takamatsu N, Nakamura M, Fuchigami M, Hata K, Sone K (2007) Secondary dispersal of *Pasania edulis* acorns by *Apodemus speciosus* into a coniferous plantation (in Japanese with English summary). *J Jpn For Soc* 89:113–120
- Iida S (2006) Dispersal patterns of *Quercus serrata* acorns by wood mice in and around canopy gaps in a temperate forest. *For Ecol Manage* 227:71–78
- Imada M, Nakai T, Nakamura T, Mabuchi T, Takahashi Y (1990) Acorn dispersal in natural stands of Mizunara (*Quercus mongolica* var. *grosseserrata*) for twenty years. *J Jpn For Soc* 72:426–430
- Imaizumi Y (1960) The mammals of Japan. Hoikusha, Osaka
- Isaji H, Sugita H (1997) Removal of fallen *Aesculus turbinata* seeds by small mammals (in Japanese with English summary). *Jpn J Ecol* 47:121–129
- Jansen PA, Bongers F, Hemerik L (2004) Seed mass and mast seeding enhance dispersal by neotropical scatter-hoarding rodent. *Ecol Monogr* 74:569–589
- Jensen TS, Nielsen OF (1986) Rodents as seed dispersers in a heath oak wood succession. *Oecologia* 70:214–221
- Kanazawa Y (1982) Some analyses of the reproduction process of a *Quercus crispula* Blume population in Nikko I. A record of acorns dispersal and seedling establishment for several years at three natural stands. *Jpn J Ecol* 32:325–331
- Kohyama T (1982) Studies on the *Abies* population of Mt. Shimagare II. Reproductive and life history traits. *Bot Mag Tokyo* 95:167–181
- Maeto K (1995) Relationship between size and mortality of *Quercus mongolica* var. *grosseserrata* acorns due to pre-dispersal infestation by frugivorous insects. *J Jpn For Soc* 77:213–219
- Miguchi H (1988) Two years of community dynamics of murid rodents after a beechnut mast year (in Japanese with English summary). *J Jpn For Soc* 70:472–480
- Miyaki M, Kikuzawa K (1988) Dispersal of *Quercus mongolica* acorns in a broadleaved deciduous forest. 2. Scatterhoarding by mice. *For Ecol Manage* 25:9–16
- Oishi K, Nakamura M, Arakaki T, Hata K, Sone K (2010) Effects of food condition on weight and breeding of wood mouse, *Apodemus speciosus* (in Japanese). *Kyushu J For Res* 63:101–104
- Podoler H, Rogers D (1975) A new regression method for the identification of key factors from life table data. *J Anim Ecol* 44:85–114
- Saitoh T, Vik JO, Stenseth NC, Takanishi T, Hayasaki S, Ishida N, Ohmori M, Morita T, Uemura S, Kadomatsu M, Osawa J, Maekawa K (2008) Effects of acorns abundance on density dependence in a Japanese wood mice (*Apodemus speciosus*) population. *Popul Ecol* 50:159–167
- Sato T (2000) Effects of rodent gnawing on the survival of current-year seedling of *Quercus crispula*. *Ecol Res* 15:335–344
- Shaw NW (1968) Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales. II. Acorn losses and germination under field condition. *J Ecol* 56:647–660
- Shimada T (2001) Hoarding behavior of two wood mouse species: Different preference for acorns of two *Fagaceae* species. *Ecol Res* 16:127–133
- Smith CC, Reichman OJ (1984) The evolution of food caching by birds and mammals. *Annu Rev Ecol Syst* 15:329–351
- Sone K, Kohno A (1996) Application of radiotelemetry to survey of acorn dispersal by *Apodemus* mice. *Ecol Res* 11:187–192
- Sone K, Kohno A (1999) Acorn hoarding by the field mouse, *Apodemus speciosus* Temminck (Rodentia: Muridae). *J For Res* 4:167–175
- Sone K, Hiroi S, Nagahama D, Ohkubo C, Nakano E, Murao S, Hata K (2002) Hoarding of acorns by granivorous mice and its role in the population processes of *Pasania edulis* (Makino) Makino. *Ecol Res* 17:553–564
- Sun S, Gao X, Chen L (2004) High acorn predation prevents the regeneration of *Quercus liaotungensis* in the Dongling mountain region of North China. *Restor Ecol* 12:335–342
- Takahashi K, Sato K, Washitani I (2006) The role of the wood mouse in *Quercus serrata* acorn dispersal in abandoned cut-over land. *For Ecol Manage* 229:120–127
- Takeda H (1992) Fruiting valuations of beech (*Fagus crenata* BLUME) trees at Nonomi beech forest for seven years (in Japanese with English summary). *J Jpn For Soc* 74:55–59
- Tamura N (1994) Application of a radio-transmitter for studying seed dispersion by animals. *J Jpn For Soc* 76:607–610
- Tamura N (2001) Walnut hoarding by the Japanese wood mouse *Apodemus speciosus* Temminck. *J For Res* 6:187–190
- Tanaka O, Kamitani T, Maruyama K (1989) Natural seedling regeneration in *Quercus mongolica* var. *grosseserrata* secondary forests and the cutting cycle of charcoal wood forest (in Japanese with English summary). *J Jpn For Soc* 71:26–30
- Ueda A, Igarashi M, Ito K (1993) Acorn infestation by insects on three evergreen oaks, *Quercus glauca*, *Q. myrsinaefolia* and *Pasania edulis*. (II). Their invasion term and level after acorn dropping (in Japanese). *Trans Jpn For Soc* 104:681–684
- Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago
- Vander Wall SB (2002) Mastling in animal-dispersed pines facilitates seed dispersal. *Ecology* 83:3508–3516
- Varley GC, Gradwell GR (1960) Key factor in population studies. *J Anim Ecol* 29:399–401
- Watts CHS (1968) The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham woods, Berkshire. *J Anim Ecol* 37:25–41
- West NE (1968) Rodent influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. *Ecology* 49:1009–1011
- Xiao Z, Jansen PA, Zhang Z (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *For Ecol Manage* 223:18–23
- Yamagawa H, Ikebuchi M, Ito S, Ito H, Hirata R (2010) Acorn dispersal by wood mice in a secondary lucidophyllous forest on a steep slope in a warm-temperate region of Japan (in Japanese with English summary). *J Jpn For Soc* 92:157–161
- Yamashita T (1994) Seed dispersal and distribution of seedlings and saplings in *Castanopsis cuspidata* var. *sieboldii* forest at its northern limit (in Japanese with English summary). *Jpn J Ecol* 44:4–19
- Yasuda M, Nakagoshi N, Takahashi F (1991) Examination of the spool-and-line method as a quantitative technique to investigate seed dispersal by rodents (in Japanese with English summary). *Jpn J Ecol* 41:257–262
- Yi X, Xiao Z, Zang Z (2008) Seed dispersal of Korean pine *Pinus koraiensis* labeled by two different tags in a northern temperate forest, northeast China. *Ecol Res* 23:379–384
- Zemanek M (1972) Food and feeding habits of rodents in a deciduous forest. *Acta Theriologica* 23:315–325