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Abstract. Dispersal and retrieval site selection by mice, transport distance, cache depth, and emergence and survival of seedlings of *Castanea crenata* (Japanese chestnut) were investigated by a magnet-locating experiment in two habitat conditions (gap vs. forest understorey). Magnets were inserted into nuts ($n = 450$) and the nuts placed in the edge of forest gaps. Although wood mice (*Apodemus speciosus* and *A. argenteus*) initially buried nuts singly in shallow surface caches near the nut source, by the following spring these cached nuts were retrieved and re-cached in larger, deeper caches farther from the source, particularly in forest understories, probably to reduce the threat of pilferage. All the nuts cached in the forest understories were consumed, but 4 seedlings emerged in gaps, apparently because of lower foraging activity in the gaps by the mice. Seed size was not correlated with cache depth or cache site selection. With increasing seed size, transport distance increased, particularly in gaps, possibly due to a greater potential energy gain (relative to handling cost to the cacher), or to attempts to prevent density- or mass-dependent loss of caches by other foragers. Variable seed dispersal behaviour based on variation in seed size may influence the chances of colonization and distribution of the light-demanding *Castanea* trees in mosaic landscapes and may play an important role in community organization and dynamics.

Keywords: Cache depth; Cache site selection; Caching behaviour; Gap; Seed dispersal; Seed mass; Transport distance; Wood mice.

Nomenclature: Ohwi & Kitagawa (1983).

Abbreviations: FU = Forest understorey; G = Gaps.

Introduction

Variation in seed size is observed among and within single plants in many plant species and this variation has been explored based on several hypotheses. Although some theoretical models have predicted a single optimum seed size (e.g. Smith & Fretwell 1974), genetic variation among seeds, seasonal changes in resource availability, and developmental or morphological constraints may prevent plants from evolving a uniform seed size (see Silvertown & Lovett Doust 1993; Sakai & Sakai 1995). Knowledge of these proximate causes of seed size variation, and the selective regime for seed size is needed to determine the ultimate causes of the seed size variation for a given species. For example, variation in seed size within a plant may be favoured in a heterogeneous environment, if optimum seed size differs among micro-environments (Janzen 1977; Howe & Richter 1982; Hendrix et al. 1991; but see McGinley et al. 1987). This suggests that several conflicting selective forces help maintain a range of seed sizes (Silvertown & Lovett Doust 1993; Moegenburg 1996). Particularly, the abilities to escape pathogens and predators, and to germinate and become successfully established, have been thought to be among the factors important in natural selection of seed size (e.g. Janzen 1969; Stanton 1985; Tripathi & Khan 1990; Cipollini & Stiles 1991; Moegenburg 1996; Bonfil 1998; Seiwa 2000; Seiwa et al. 2002).

Seed dispersal has been identified as an adaptive trait for seedling establishment, due to (1) disproportionate success of seed and seedlings that escape density-dependent fungi and herbivore attack in the vicinity of the parents, as compared with those dispersed nearby (Janzen 1970; Howe & Smallwood 1982; Augspurger & Kelly 1984; Clark & Clark 1984; Tomita et al. 2002), and (2) increased probability of reaching local sites suitable for establishment (Howe & Smallwood 1982). Past studies have revealed that seed size influences seed dispersal behaviour of small mammals (e.g. squirrel and wood mice). Large seeds were preferred, being harvested earlier or dispersed more widely than small ones

(e.g. Jensen 1985; Uhl 1987; Wilson & Whelan 1990; Myster & Pickett 1993; Van der Wall 1994a; Miguchi 1996; Seiwa & Kikuzawa 1996). These studies, however, compared species differing in seed sizes. Little is known about how variation in seed size within a species influences seed dispersal behaviour (i.e. dispersal distance, caching depth, cache size, and cache site selection) of small mammals.

Post- and pre-dispersal seed predation by rodent scatter hoarding has implications for the fate of seeds and seedling establishment success in a variety of communities (e.g. Stapanian & Smith 1978; Miyaki & Kikuzawa 1988; Van der Wall 1994b). Differences in vegetation structure and/or composition in forests also influence seed predation and dispersal behaviour. Different seed dispersers (predators) prefer certain microhabitats to others, and seed predation is often heterogeneous, resulting in spatially heterogeneous seedling emergence (e.g. Uhl 1987; Miyaki & Kikuzawa 1988; Bowers & Dooley 1993; Van der Wall 1994b; Hoshizaki et al. 1997; Abe et al. 2000). In temperate forests, wood mice (e.g. *Apodemus* spp.) are rarely active far from vegetation cover (canopy trees, shrubs and dwarf bamboo), thus limiting seed dispersal into open habitats such as gaps and forest edges (Miyaki & Kikuzawa 1988; Kikuzawa 1988; Wada 1993); conversely jays and squirrels store seeds in open habitats, contributing to their invasion by seed-bearing trees (Nakamura 1984; Miyaki 1987; Hayashida 1991). However, wood mice are usually more abundant and active compared with other seed dispersers in temperate forests in Japan (e.g. Kikuzawa 1988; Miguchi 1996). Thus, it remains uncertain how such light demanding large-seeded forest species invade open habitats where there is little vegetation cover.

Castanea crenata (Japanese chestnut; *Fagaceae*) is a shade intolerant, early successional deciduous broad-leaved tree species commonly found in temperate Japan (Seiwa & Kikuzawa 1991; Watanabe et al. 1996). It regenerates successfully only at sunny sites such as gaps and forest edges (Masaki et al. 1992; Tamura & Seiwa unpubl. data). However this situation may be a reflection of seed predator behaviour rather than the autecology of the chestnut species.

To detect the effect of seed size and habitat conditions (gap vs. forest understorey) on seed dispersal and seedling establishment of *C. crenata*, we used a magnet-locating method to determine the fate of seeds in artificially created gaps. We have 3 questions. 1. To what extent do seed size and habitat conditions affect caching behaviour (dispersal site selection, transport distance, cache depth and cache size) of the seed disperser? 2. How does caching behaviour influence seedling establishment. 3. Do the results help explain the maintenance of seed size variation in this species?

Methods

Study area

This study was conducted in a broad-leaved deciduous forest in the experimental forest of Tohoku University in northeast Japan (38° 48' N, 140° 45' E). From mid-December 1995 to mid-April 1996, there was snow cover to a maximum depth of 165 cm. Mean monthly temperature during the same period ranged from $-1.8°C$ (January) to 23.0 °C (August). Mean annual temperature and rainfall were 9.8 °C and 2140 mm, respectively. The soil is a silty, well-drained andosol (Anon. 1974).

Ca. 168 ha have been protected from human activity for at least 30 yr as a forest preserve. Trees in the study forest have re-established since clear-cutting 50 yr ago. The mean and maximum heights of trees forming the forest canopy were 15 m and 18 m, respectively. The canopy layer in this forest was dominated by *Quercus serrata*. *Rhododendron obtusum* var. *kaempferi*, *Elliottia paniculata*, while *Sasa palmata* were dominant in the understorey layer. For the study, 3 artificial gaps (6 m in radius) were created in the forest by felling the trees on a ridge area with a gentle slope (< 2°) at 500 - 530 m above sea level in November 1995. Gaps were separated from each other by more than 85 m and were more than 150 m away from the nearest mature *Castanea* tree.

Seed tracking

Since metal- or magnet-inserted acorns are easily detected by metal-detector, and since the magnet-locating method is effective for tracking seeds dispersed by small mammals (Sork 1984; Iida 1996), we employed it to detect the nuts after their dispersal. Nuts were haphazardly collected from 3 trees outside the study forest. The nuts were floated in water for 24 hr to eliminate empty ones. Nuts with obvious insect damage were also discarded. There was wide variation in seed mass (mean = 3.91 g, range = 1.1 - 10.8 g, $n = 848$). Each nut was drilled with a hand drill into the side opposite the embryo, so as not to prevent germination. A small ferrite magnet (8 mm in diameter, 3 mm in thickness, surface magnet flux density of 1000 Gs) was inserted into the drill hole. The mass of a magnet was 1 g. Each nut was marked with a serial number, in one of 3 different colours according to 3 seed-size classes. The nuts were then classified into 3 mass classes with average (± SE) nut masses of large, 6.52 ± 0.08 g ($n = 150$), medium, 3.96 ± 0.02 g ($n = 150$), and small, 2.54 ± 0.03 g ($n = 150$). On 18 November 1996, we placed 150 nuts with their inserted magnets (50 nuts per each nut mass class) on the ground within a circle of 1.0 m in diameter on the edge of each of 3 forest gaps (the 'drop zone'), and left

these for animal dispersal. A magnet-locator (GA-52B, Schonstedt Instrument Company, Virginia, USA) was used to investigate the location of the dispersed nuts. This census was conducted within 3 quadrats each 60 m × 60 m, which were centred on the 3 drop zones. This census was conducted intensely and carefully, particularly in gaps, to insure that a minimum number of nuts would be overlooked. The investigation of the fate of the nuts was conducted twice: (1) 2 days after placement of the nuts; (2) the following spring, immediately after snowmelt on 21 and 22 April 1997. Number, spatial location and burial depth of identified nuts were recorded before reburial.

To identify potential nut transporters and their density and home ranges during this experiment, 25 Sherman live-traps baited with peanuts were regularly spaced at 10-m intervals in 40 m × 40 m areas (the central area of each quadrat). Captured animals were finger-cut for individual identification, weighed, classified (by species and sex), and released at the point of capture. This census was conducted on 26, 27 and 28 Nov. 1996 and on 27 and 28 May 1997.

Seedling emergence was investigated on 24 June 1997 in the 3 quadrats, 2 months after snow melt. Seedling survival was also investigated on 8 occasions at 3 - 5 mo intervals until November 1999.

Statistical analysis

Since nuts can only be dispersed short distance into gaps (G) compared with forest understories (FU), the seed fate characteristics (transport distance, cache site location, cache depth, and cache size) were analysed separately in each habitat. Transport distance and cache depth were contrasted among nut size classes and between 2 observed times (November 1996 vs. April 1997) by two-way ANOVA that included block (3 replicate sites) effects. Transport distance observed in April 1997 was defined as the linear distance from the starting point (centre of the drop-zone). After consumption of the nuts by predators, we could often identify the nut size by observing the coloured serial numbers on the nut shells or their fragments beside the magnets. However, we could not identify the nut size for 92 magnets (44% of total magnets observed). The magnets were tightly inserted into the nuts so that they couldn't fall out, and thus they were sure to be located at the place rodents ate the nuts. So for nuts not consumed on the surface, but in burrows etc, we could determine the cache depth as the depth of the magnet found. Therefore, transport distance and cache depth were again analysed in FU and G, separately, by one-way ANOVA of data pooled across 3 nut mass classes including magnets not identified as to size class. Cache

size (number of nuts per cache) was also analysed by one-way ANOVA in FU but not in G, since the nuts were cached singly at both times (see Results). To evaluate whether wood mice choose particular nut sizes, the number of nuts dispersed were compared among nut mass classes in each habitat separately by one-way ANOVA in each observation period. Data were log- (transport distance and cache depth) or square root-transformed (cache size) to meet assumptions of the ANOVA (Bartlett test).

Results

Nuts dispersers

The mice species *Apodemus speciosus* and *A. argenteus* were captured in the study area. The mean numbers of previously uncaptured *A. speciosus* and *A. argenteus* captured per quadrat were 1.6 and 0.7 day^{-1} in November 1996, respectively, and 1.2 and 4.4 day^{-1} in April 1996, respectively, using 25 live-traps. Nut shell fragments with rodent teethmarks were also frequently observed beside magnets. Thus, these 2 mice species appeared major nut dispersers and consumers of the nuts of *Castanea crenata* in this study area.

Difference in the fate of nuts between gaps and forest understories

The fate of nuts from the time they were artificially placed in the gap edge is shown in Fig. 1. The data were pooled across 3 nut mass classes in the 3 study quadrats. All 450 nuts inserted with magnets disappeared from the replicate drop zones within 2 days. At that time, 75 (16.7%) of magnet-inserted nuts (40 nuts in G, 35 nuts in FU) and 13 (2.9%) magnets without nuts (1 in G, 12 in FU) were relocated. Presumably, 80.4% of nuts have been transported off the quadrats and/or were undetected. During the winter from Nov. 1996 to April 1997, 29 (6.4%) nuts cached in G were transported into FU, while 7 (1.6%) nuts cached in FU were transported into G. The number and proportion of nuts consumed by mice during winter was greater in FU ($n = 87$, 19.3%) than in G ($n = 4$, 0.9%). Consequently, the number of nuts which survived was greater in G ($n = 14$, 3.1%) than in FU ($n = 9$, 2.0%) in April 1997. On 24 June 1997, although no seedlings had emerged in FU, 4 (0.89%) seedlings emerged in G. 3 (0.67%) seedlings were still alife after 29 months (till November of 1999).
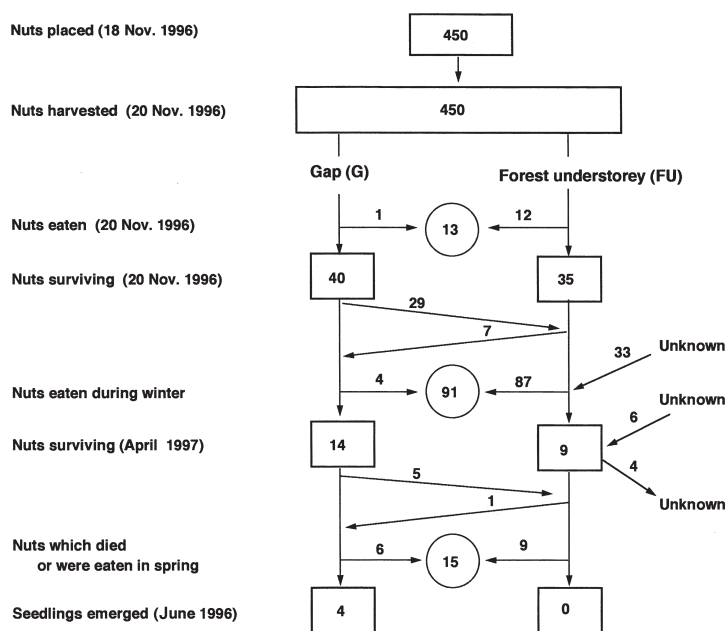
Fig. 1. Pathways of chestnuts placed on the edge of the gap (G) at the experimental sites. Data were pooled across 3 replicates.

Transport distance

Transport distance was usually greater in FU than G. This phenomenon would be in part affected by the experimental design so that maximum potential distance from the drop-zone to the gap was shorter than that to the forest understory. Two-way ANOVA showed that transport distance was not affected by the time of observation (Nov. 1996 vs. April 1997) in both FU and G, but was significantly affected by nut mass in G (Table 1). Then, transport distance was usually longest for largest nuts and shortest for smallest nuts (Fig. 2A). In FU, transport distance was slightly greater (though not statistically significant) for larger nuts in November 1996, but the trend diminished in April 1997. When data were pooled across all nut mass classes, including magnets not identified as to size class, transport distance significantly increased with time in FU but not in G (Table 2, Fig. 2B). In FU, the most frequent and maximum transport distances were for the classes of 5 - 10 m and 20 - 25 m, respectively, in November 1996, but 10 - 15 m and 30 - 35 m, respectively, in April 1997 (Fig. 2B).

Cache depth

Cache depth of the nuts was significantly affected by time of observation, but not affected by nut mass. There was no interaction between the factors in either FU and G (Table 1). When data were pooled across the 3 nut mass classes, including magnets not identified as to size class, cache depth was significantly affected by time in each habitat (Table 2). Caching depth did not differ among nut mass classes at each time and habitat (Fig. 2A), but was usually deeper in FU than in G at each time, and increased with time in FU but not in G (Fig. 2B). Although the nuts were buried at various depths (0 - 75 cm) in FU, all these nuts were eaten. Seedling emergence occurred only from the nuts buried at shallow depth (0 - 10 cm) in G.

Nut size preference

In both FU and G, the number of nuts dispersed was not significantly different among nut mass classes in both November 1996 and April 1997 (one-way ANOVA, $F < 3.717$, $p > 0.103$), implying that wood mice did not prefer to disperse particular sizes of nuts in each habitat.

Table 1. Effects of nut mass and time of observation (Nov. 1996 vs. April 1997) on transport distance and cache of chestnuts (*Castanea crenata*), by two-way ANOVA.

| | | Transport distance | | | | Cache dept | | | |
| | | Forest understorey | | Gap | | Forest understorey | | Gap | |
	df	F-ratio	P	F-ratio	P	F-ratio	P	F-ratio	P
Nut mass	2	0.48	N.S.	8.98	< 0.001	0.10	N.S.	0.33	N.S.
Time	1	2.55	N.S.	0.75	N.S.	4.44	0.041	16.45	< 0.001
Nut mass × time	2	0.96	N.S.	0.14	N.S.	0.19	N.S.	0.64	N.S.
Block	2	22.55	< 0.0001	4.27	0.020	3.67	0.034	4.31	0.019
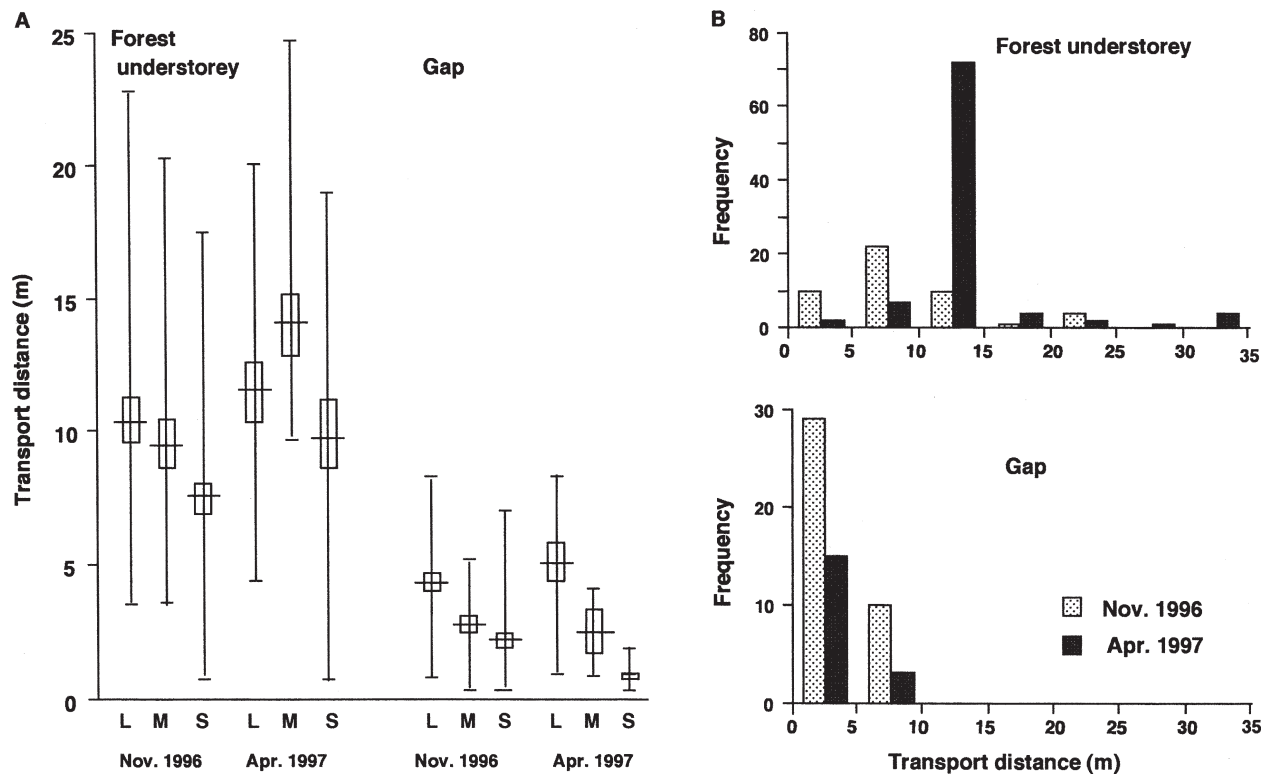
Fig. 2. A. Transport distance of chestnuts of three different nut mass classes (L = large; M = medium; S = small) in November 1996 and April 1997 in the forest understorey (FU) and the gap (G). Horizontal bar = mean; Box = ± SE, Vertical line = range. **B.** Differences in dispersal distance of chestnuts up to 2 survey times, November 1996 and April 1997 in FU and G regardless of nut mass.

*Relationships among transport distance, cache depth and cache size*

While all of the nuts were cached singly at both times (November 1996 and April 1997) in G, cache size increased with time in FU (Fig. 4). In the latter, although only one cache included 2 nuts in November 1996, 35% of caches (*n* = 14) included 2 to 13 nuts in April 1997. Thus, one-way ANOVA showed significant effects of time on cache size in FU (Table 2). Caching depth generally increased with increasing transport distance in both November 1996 (Spearman rank correlation coefficient, r_{sp} = 0.360, *p* = 0.0021) and April 1997 (r_{sp} =

0.365, *p* < 0.0001; Fig. 4). Although nuts were cached at a shallow depth in November 1996, most of the nuts were re-cached at greater depths in larger caches in April 1997, showing a shift from surface caches to burrow and nest caches with time course. In the area 10 to 15 m away from the drop zone in FU, there were several large caches at greater depth, due to burrow and nest caches.

Table 2. Effects of time of observation (Nov. 1996 vs. April 1997) on transport distance, cache depth and cache size (number of nuts per cache) of chestnuts (*Castanea crenata*). Data are pooled across three nut mass classes so as to include magnents without nuts, by one-way ANOVA.

| | | Transport distance | | | | Cache dept | | | | Cache size | |
| | | Forest understorey | | Gap | | Forest understorey | | Gap | | Forest understorey | |
	df	F ratio	*P*	F ratio	*P*	F ratio	*P*	F ratio	*P*	F ratio	*P*
Time	1	20.81	< 0.0001	2.13	N.S.	34.99	< 0.0001	24.63	< 0.0001	12.32	< 0.0001
Block	2	14.96	< 0.0001	3.63	0.033	15.03	< 0.0001	3.83	0.028	11.79	< 0.0001
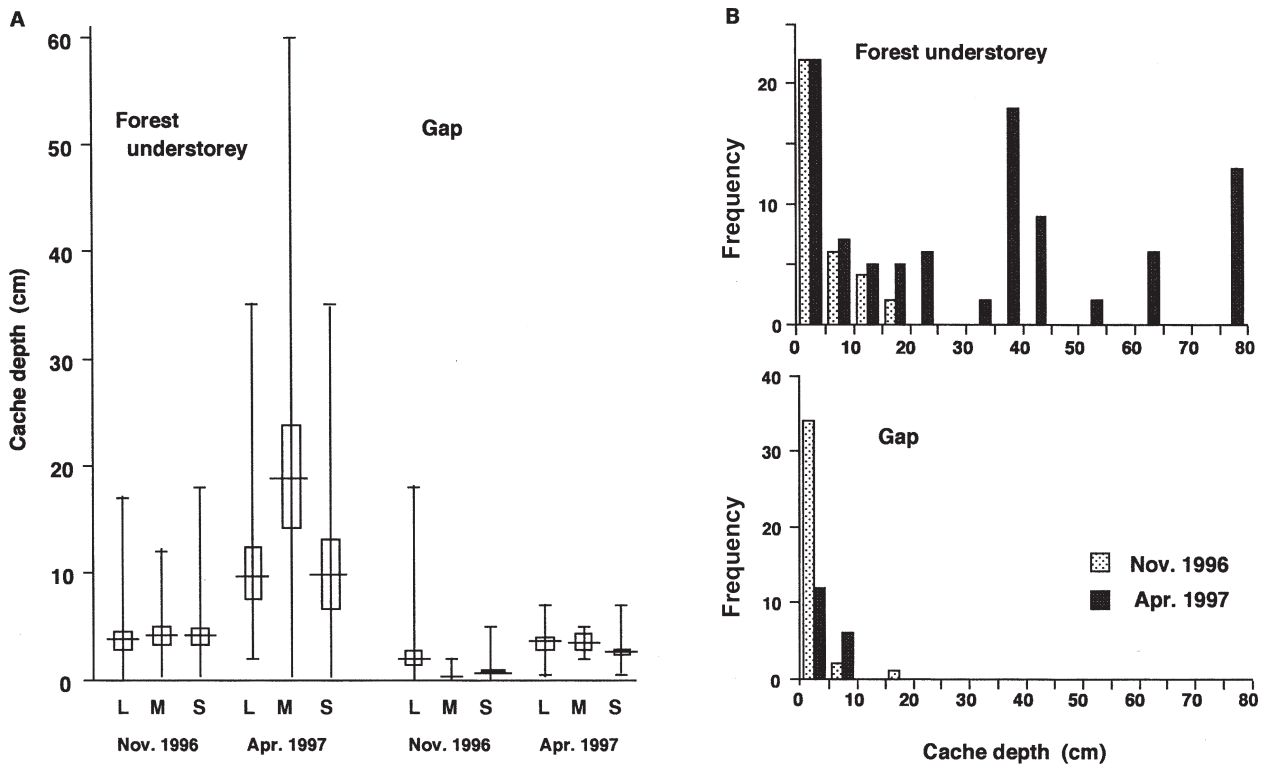
Fig. 3. A. Cache depth of chestnuts of three different nut mass classes (L = large; M = medium; S = small) in November 1996 and April 1997 in the forest understorey (FU) and the gap (G). Horizontal bar = mean, box = ± SE, vertical line = range. **B.** Differences in cache depth at 2 survey times, November 1996 and April 1997 in FU and G, regardless of nut mass.

Discussion

Importance of cache and retrieval site selection on the establishment success of chestnuts

This study revealed that the caching behaviour of 2 wood mice species was substantially different between gaps and forest understories and was also changed significantly with time after the nuts became available, these factors having a great influence on the seedling establishment success of *Castanea crenata*.

Although wood mice initially cached nuts singly and buried them in shallow caches near the source, nuts were subsequently retrieved and cached again in much larger caches, at greater depth and farther from the source. Soné & Khono (1999) conducted a more frequent investigation using radiotelemetry; they revealed that *Apodemus* species retrieved, transported and hoarded acorns a maximum of 7 × and that the acorns were hoarded farther from the food stations with increasing hoading sequence. Since the home ranges of resident mice overlap significantly in *A. speciosus* (Oka 1992), there is an advantage for the mice initially to keep surplus food by scatter-hoarding so as to reduce the

threat of pilferage of cached nuts, and then to transport them to a place much farther from the food source to reduce detection by competitive naive foragers (Stapanian & Smith 1978; Van der Wall 1993) or density dependent caching loss (Clarkson et al. 1986). Cache depth also increased with time in this study. This trait showed a shift from surface caches to larder (burrow and nest) caches with time, and indicated the adaptive advantage for the mice in escaping detection by competitive foragers.

In contrast to previous studies on cache site selection of wood mice in temperate forests (e.g. Miyaki & Kikuzawa 1988; Quintana-Ascencio et al. 1992; Wada 1993), this magnet-locating investigation of seed fate in *C. crenata* showed that a large number of the nuts were dispersed not only in FU but also in G by the wood mice species. Surprisingly, seedling emergence was observed only in G but not in FU. Such gap biased seedling emergence is perhaps due to the fact that there was little nut-retrieval activity in G compared with FU for the foraging mice. It is well known that rodent activity is reduced in microhabitats with low vegetation cover, particularly during bright nights (Jensen & Nielsen 1986; Kikuzawa 1988; Bowers 1990; Quintana-Ascencio et
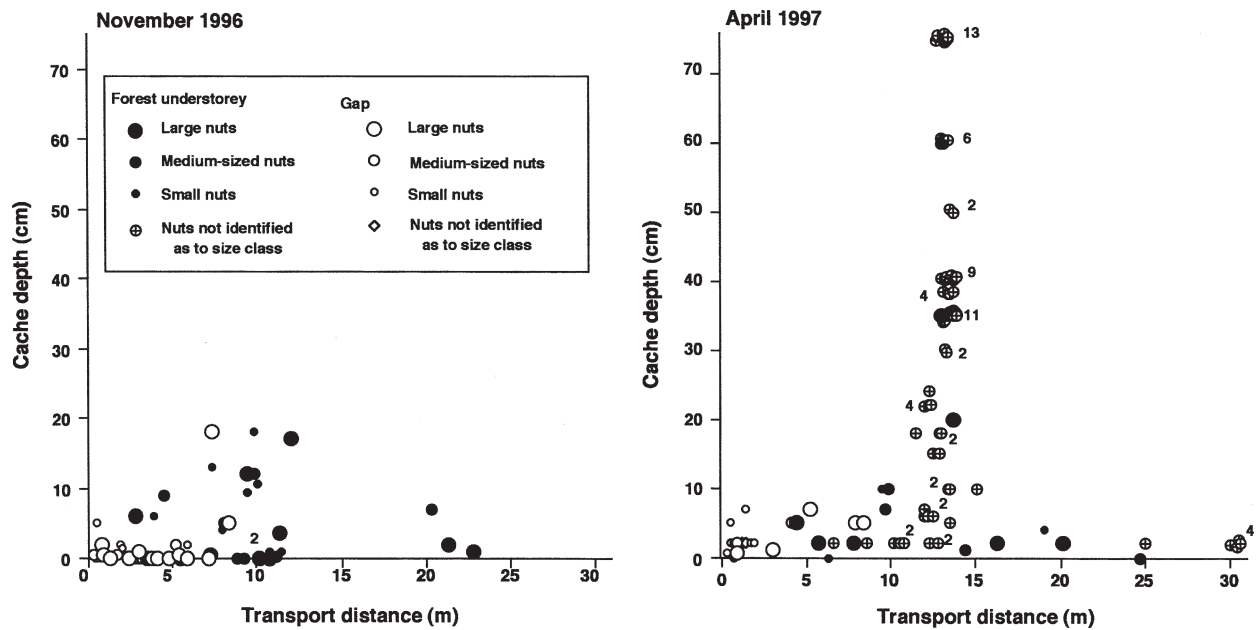
Fig. 4. Relationships between transport distance and cache depth in November 1996 and April 1997. Numerals beside symbols indicate the number of nuts per cache.

al. 1992; Bowers & Dooley 1993; Wada 1993; Forget 1997). A thin vegetation cover also provides the rodents with few hiding places from predators (mostly birds such as owls) (Miyaki & Kikuzawa 1988; Bowers 1990; Quintana-Ascencio et al. 1992; Bowers & Dooley 1993). Therefore, the establishment success of the chestnuts would be determined by risk-avoiding behaviour of the foraging mice, which did not favour retrieval and feeding on the nuts in G with little vegetation cover. In contrast, all of the nuts dispersed into FU were consumed by foragers, resulting in no seedling emergence.

These caching and retrieval behaviours of the wood mice seem to be adaptive for seedling establishment of Japanese chestnuts, since the chestnuts are 'gap regenerators', growing and surviving well in sunny habitats (Masaki et al. 1992; Watanabe et al. 1996). Greater probability of seedling emergence in gaps due to little retrieval activity would in part explain the reason why saplings and juvenile trees of *C. crenata* are seldom observed in forest understories compared with gaps and forest edge (Tamura & Seiwa unpubl. data). Differences in nut caching and retrieval rates between habitats may influence the chances of invasion and distribution of chestnut trees in mosaic landscapes, and may play an important role in affecting the community organization and dynamics.

Importance of nut-size variation on seedling establishment in variable environments

Preference for different seed sizes has been reported among species in several communities (Price 1983; Jensen 1985; Jensen & Nielsen 1986; Uhl 1987; Willson & Whelan 1990; Myster & Pickett 1993; Van der Wall 1994a), Few studies, however, have been conducted on how variation of seed size within a species influences seed caching behaviour in field conditions, although size-selective seed preference by rodents has been observed in the laboratory (Price 1983). In this study, although there was little evidence that larger nuts were preferentially dispersed, dispersal distance increased with increasing nut mass particularly in gaps. Even in FU, transport distance was slightly longer for larger nuts in the early phase of seed dispersal. These phenomena demonstrates that caching behaviour of woody mice is greatly affected by seed size within a species in natural forest conditions. However, the effect of nut size diminished with time, probably since caching behaviour of wood mice in the later phase of dispersal would be strongly affected by the location of their home range and the chances of successfully re-caching nuts, both of which are independent of nut size. Nut-size dependent transport distance can be explained by the cost-benefit model (Pulliam 1974; Stapanian & Smith 1978). When not taking the influence of competitive foragers into consideration, this model predicts that seed dispersal distance is determined by the balance of the benefit from

a seed (energy content) against the cost of carrying or hoarding. Average dispersal distance would increase with increasing nut mass, probably due to the disproportionate increase of the benefit against the transport cost to the cacher. Alternatively, farther transport of larger nuts would also be predicted by the density-dependent cache loss model of Clarkson et al. (1986). They predicted that if density-dependent loss of caches to other foragers is high, then caches should be placed at lower density (greater transport distance). Soné & Khono (1996) found a similar phenomenon, namely, that *A. speciosus* dispersed transmitter-installed acorns much farther from the site of placement than acorns without transmitters, probably due to the heavier mass (perceived greater benefit) of the former. Longer dispersal distance would provide several adaptive advantages for larger nuts in *C. crenata*. Large nuts may have a greater probability of escaping from pathogen and herbivore attacks which are intense near conspecific adults, even in temperate forests (Shibata & Nakashizuka 1995; Maeto & Fukuyama 1997; Murakami & Wada 1997; Tomita et al. 2002). Moreover, longer dispersal distance would enhance the chance of recruitment into safe sites such as gaps (Howe & Smallwood 1982; Shibata & Nakashizuka 1995; but see Sakai et al. 1998), or reduce the sib-competition within a safe site (Murray 1988) for large nuts.

Cache depth was independent of nut mass, and all of the nuts which were buried 10 cm below the ground surface were predated irrespective of nut mass. Thus effects of nut mass on the seedling establishment could be evaluated by comparing the seedling performance from the nuts of various sizes in shallow burial. In a nut burial experiment in nursery conditions, and in the absence of foraging animals, when nuts were buried to less than 10 cm depth, both seedling emergence and seedling height were not influenced by nut mass, although in deeper soil only large nuts became successfully established (Seiwa et al. 2002). These phenomena suggest that larger nut mass has little benefit for seedling establishment of chestnuts as wood mice consumed most of these nuts cached at greater depth (cf. nest and burrow hoarding).

Although *C. crenata* seedlings from heavy nuts grew better than those from light ones in nutrient-poor conditions, the nut mass effects did not persist beyond the early phase of the growing season in nutrient-rich conditions (Watanabe et al. 1996; Seiwa et al. 2002). Stable isotope (^{15}N) experiments revealed that small-seeded chestnut seedlings rapidly absorbed nitrogen from soil and then had nitrogen-rich leaves, resulting in greater Relative Growth Rate than large-seeded ones under nitrogen-rich conditions (Seiwa & Watanabe unpubl. data). These traits imply that parental fitness increases

when small seeds are produced under particular conditions, since a greater number of small seeds can be produced by a parent with limited resources (Smith & Fretwell 1974). In turn, large seeds would not always have an adaptive advantage over small seeds, since environmental nutrient conditions are spatially and temporally heterogeneous and unpredictable in both temperate and tropical forests (Lechowicz & Bell 1991; Denslow et al. 1998; Denslow & Guzman 2000; Topoliantz & Ponge 2000). Maintenance of seed-size variation may be an adaptation of *C. crenata,* promoting farther seed dispersal and seedling vigour in nutrient-poor conditions for larger seeds, and compensatory vigour for small seeds in nutrient-rich conditions.

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