15 Mast Seeding and Predator-mediated Indirect Interactions in a Forest Community: Evidence from Post-dispersal Fate of Rodent-generated Caches

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Introduction

When and how do seeds die? For most temperate trees the answer is soon after seed fall and as a result of seed predation. In temperate deciduous woodland a considerable proportion of seeds is consumed by granivores (Hulme, 1993, 1998; Hulme and Benkman, 2001). Not surprisingly, granivores (in particular, small mammals) have been found to play a pivotal role in the regeneration (Hulme, 1996b, 1997), colonization ability (Myster and Pickett, 1993), spatial distribution (Kollmann, 1995) and reproductive ecology (Sork, 1993) of temperate trees. To date, research on granivory in deciduous woodlands has tended to focus on the relative importance of habitat, microhabitat, plant species and seed density for seed predation rates (Willson and Whelan, 1990; Whelan *et al.*, 1991; Myster and Pickett, 1993; Hulme and Borelli, 1999). However, the frequent absence of consistent directional trends (e.g. Willson and Whelan, 1990) has made it difficult to construct accurate predictive models of post-dispersal seed predation. One factor that might lead to inconsistencies in seed-predation rates may be the temporal and spatial variation in the abundance of alternative food resources.

Polyphagous seed predators, such as small mammals, are likely to respond not only to the absolute abundance of a particular seed species but also to its relative abundance in relation to other seed species (Greenwood, 1985). For example, the rate of seed predation on a particular plant species can decrease dramatically following an increase in availability of a more preferred species. Such frequency-dependent foraging by granivores has considerable potential to structure plant communities (Hulme, 1996a). Furthermore, frequency dependence may explain why inconsistent trends in removal rates are sometimes found among habitats, seasons and years (Schupp, 1990; Willson and Whelan, 1990; Kollmann *et al.*, 1998). These inconsistencies may simply reflect spatial and/or temporal changes in the relative abundance of different seed species. Although several studies have examined seed predation in a community context (Schupp, 1990; Kollmann *et al.*, 1998), only Hulme and Hunt (1999) have analysed how a seed

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predator's preference depends on the relative abundance of two species.

In addition to functional changes in rodent foraging behaviour as a result of variation in seed frequency, granivores may also respond numerically to variation in seed abundance (Ostfeld *et al.*, 1996; Ostfeld and Keesing, 2000). A build-up in granivore abundance may occur following an increase in the density of the seeds of one plant species. If granivores forage in a frequency-independent manner, an increase in rodent abundance may lead to an increase in absolute rates of seed predation on the seeds of all plant species in the community but should not alter the relative removal of different species. However, the effect on the less abundant plant species may be disproportionate if they are more vulnerable to the increased impacts of granivores (e.g. recruitment more seed-limited) (see Hulme, this volume).

The impact of variation in seed abundance on seed predation is most likely to be found in plant communities dominated by species that produce large, synchronous seed crops at irregular intervals (e.g. masting species). Mast seeding in tree species and the consequent satiation of seed predators have long been a phenomenon of particular interest (e.g. Janzen, 1971). However, few studies have examined the consequence of masting on the seed/seedling survivorship of co-occurring non-masting trees (but see Curran and Webb, 2000). To what extent, then, does annual variation in seed production among species influence populations of generalist predators and, consequently, their pattern of seed predation?

Indirect interactions often play significant roles in community dynamics (Wootton, 1994; Morin, 1999). Indirect interactions may apply to tree species and their seed predators, because many seed predators are generalists (Crawley, 1992) and respond numerically to seed abundance (Ostfeld *et al.*, 1996; Ostfeld and Keesing, 2000). Temporal variation in seed production by one tree species is expected to have an impact on seed predation on co-occurring species. This type of indirect interaction remains unexplored in seed-predation studies.

Within this context we examined the impact of temporal variations in seed supply on rates of seed removal by rodents. Our goal is to demonstrate that seed predation on *Aesculus turbinata* can depend on the seed abundance of other dominant tree species. In particular, we explore the impact of seasonal variation in *Fagus crenata* seed fall. This is a particularly suitable system to study, since *F. crenata* produces large, irregular mast crops of seeds that are highly preferred by rodents. To examine how masting indirectly affects seed predation in *A. turbinata*, we addressed the following questions:

1. Are rates of *A. turbinata* seed predation indirectly affected by the seed fall of *F. crenata*?
2. Within a mast year, is the effect of *F. crenata* on *A. turbinata* consistent among seasons?
3. What most determines the overall success of *A. turbinata* seeds – its own seed fall or that of *F. crenata*?
4. Do seed predators respond equally to annual variation in seed production of *A. turbinata* and *F. crenata*?

Study Species and Sites

The natural history of *A. turbinata* (*Hippocastanaceae*), a deciduous canopy tree, is described in detail in Hoshizaki *et al.* (1997, 1999). Its seeds are particularly large (2–4 cm in diameter) and contain more seed reserves (6.2 g per seed, dry mass (Hoshizaki *et al.*, 1997)) than any other seeds in the temperate forests of Japan and perhaps in all northern temperate forests. Seed fall begins in mid-September and continues until the beginning of October. The principal granivores of *A. turbinata* are small mammals (*Apodemus speciosus* and *Eothenomys andersoni*). They readily take fallen seeds and either consume or cache them (Hoshizaki, 1999). Spatial variation in seed removal by rodents is low (Hoshizaki *et al.*, 1999), whereas temporal variation is high (Hoshizaki *et al.*, 1997). Caching increases the probability of seeds reaching sites suitable for establishment, because it enlarges the seed shadow (Hoshizaki *et al.*, 1999).

At our study site in the Kanumazawa Riparian Research Forest (39° N, 140° E) (see Hoshizaki *et al.* (1997) and Suzuki *et al.* (2001) for a detailed description), *A. turbinata* occurs with two other common tree species, which also display large interannual variation in seed production. *Fagus crenata* (*Fagaceae*) is overwhelmingly dominant and exhibits strict masting cycles (*sensu* Kelly, 1994; see also Miguchi, 1988, 1996). Annual variation of seed production in a second species, *Quercus mongolica* var. *grosseserrata* (*Fagaceae*), is less synchronized and more regular (Miguchi, 1996; see also Sork, 1993). The seeds of the three species differ in both the quality and quantity of resource they present to rodents. Seeds of *A. turbinata* contain saponins and tannins, seeds of *Q. mongolica* (seed mass, 1.7 g) contain tannins and no saponins and seeds of *F. crenata* (0.13 g) contain no tannins or saponins (K. Hoshizaki, unpublished data).

Research was undertaken in two sites within the Kanumazawa Riparian Research Forest. The long-term monitoring plot represented a 1 ha site in which the seed fall and germination of *A. turbinata* and *F. crenata* have been studied for 7 years (1992–1999). To interpret the long-term trends, a 0.4 ha short-term experimental plot, 150 m from the long-term monitoring plot was established in 1995. The short-term experimental plot was used to examine rates of *A. turbinata* and *F. crenata* seed removal.

Methods

Long-term annual variation in seed predation and seedling establishment

Seed production of the three tree species (*A. turbinata*, *F. crenata* and *Q. mongolica*) was recorded annually from 1992 to 1998 in the long-term monitoring plot. Between 99 and 121 seed traps were established at regular 10 m intervals throughout the plot in each year. Each seed trap comprised a nylon-mesh bag (1 mm mesh) with a receiving area of 0.5 m^2, set 1.2 m above the ground. Seeds were collected from all traps every 2 weeks. In early June each year, all new *A. turbinata* seedlings within the long-term plot were tagged and their locations mapped. Because *A. turbinata* has no dormancy, overall seed survival can be estimated from the ratio of newly germinated seedlings to seed fall in the previous autumn. We measured seed success as both the proportion and the total number of *A. turbinata* seeds that successfully produced seedlings.

To test whether the annual variation in seed predation in *A. turbinata* is related to seed abundance, we examined *A. turbinata* seed success in relation to the abundance of seeds in the previous autumn. These analyses were also undertaken in relation to variations in seed production of *Fagus* and *Quercus* in order to examine the effects of seed production by other tree species on *A. turbinata* seed success. These data were also interpreted in relation to community-wide food abundance for rodents. The community-wide food abundance, measured as seed-fall energy per hectare, was estimated as the summed value of total seed-fall biomass multiplied by the per-gram energy for each species (K. Hoshizaki, unpublished data).

Short-term assessments of A. turbinata *and* F. crenata *seed predation*

In each of 3 years (1995–1997) we followed the fate of *c.* 100 seeds of *A. turbinata* placed under each of five mature trees in the short-term plot. In 1995 and 1996 all seeds came from under these same trees; however, in 1997 seed production was especially low and seeds from other trees also had to be used. Each September, we attached one end of a 40 cm length of wire to a seed and the other end to coloured tape. The number of seeds to which a wire was attached on any one day was determined by the daily seed fall. Every 2–7 days until seedling emergence the following spring (except for a period with snow cover), we searched for marked seeds, as described in Hoshizaki *et al.* (1999). We recorded seed location and status (cached, germinated or eaten). In most cases we could find the seeds because the coloured flag was rarely buried and because the wire was never severed. The mass of the wire (*c.* 2 g) was small compared with the mass of the seeds (*c.* 19 g).

Ideally, predation on *F. crenata* seeds should be evaluated by tracing the fate of seeds as we did for *A. turbinata*. However, due to the relatively small seed size of *F. crenata*, attaching a length of wire to seeds would more than likely influence rodent foraging behaviour. Therefore, *F. crenata* seed predation was assessed indirectly. Under each of two *F. crenata* trees, we established three sample plots. Each plot consisted of four 50 cm × 50 cm quadrats and an adjacent seed trap (see above for description). From October until mid-November in 1995 (a mast year for *F. crenata*), we collected *F. crenata* seeds in a litter sample from one of the four quadrats in each plot every 2 weeks. During the same period and at fortnightly intervals, all *F. crenata* seeds in seed traps were also collected and counted. Daily removal rate (R) of *F. crenata* seeds was calculated as:

$$R = \frac{(G_i + F_{i-j}) - G_j}{t_j - t_i} \qquad (1)$$

where G_i is the number of *F. crenata* seeds in the litter at time t_i, G_j is the number of seeds in the subsequent litter sample at time t_j, and $F_{i\text{-}j}$ is the number of seeds that were collected in the seed trap during the period t_i to t_j. Seed numbers were standardized to seeds per m^2 before calculation. We assume that this removal rate is equivalent to seed consumption rate.

In September 1995, we established an array of seed traps ($n = 69$) to monitor the rate of seed fall for *Fagus* in a 10 m spacing grid in and around the short-term study plot. We collected the contents of traps approximately every 2 weeks and counted sound seeds. The phenology of *Aesculus* seed fall was estimated from the number of seeds tagged per day during the fruiting period. Seedling emergence of both *F. crenata* and *A. turbinata* was assessed following the methodology described for the long-term monitoring plot.

Seed-predator census

We monitored populations of *A. speciosus* and *E. andersoni* from the autumn of 1994 to the autumn of 1999. Rodents were censused between two and five times each year, using Sherman live traps placed 10 m apart in a 4 × 6 or 5 × 8 grid within the Kanumazawa Riparian Research Forest and close to the long- and short-term plots. Each census consisted of three consecutive nights of trapping. Traps were baited with sweet potato and sunflower seeds and checked daily. Rodents were toe-clipped for individual identification and released at the site of capture after species and sex had been recorded. Population density was conservatively estimated as the minimum number alive (MNA) for each species during each trapping session.

Data Analysis

Frequency-dependent seed predation

To test the idea that removal of *A. turbinata* seeds was reduced by *F. crenata* seed fall due to rodents shifting their food resources to the preferred seed, we examined the degree of frequency dependence in seed removal (Hulme and Hunt, 1999). Analysis of frequency dependence followed the method proposed by Greenwood and Elton (1979). Suppose that A_1 and A_2 are the densities of prey1 (*F. crenata*) and pray2 (*A. turbinata*) available and E_1 and E_2 are the densities consumed, a relationship may be fitted between the ratios of frequencies available and consumed, such that:

$$\frac{E_1}{E_2} = \left(v \frac{A_1}{A_2} \right)^b \qquad (2)$$

The constant b is a measure of frequency dependence: if it is greater than one, granivores consume proportionally more of the common prey; if it is less than one, granivores consume proportionally less of the common prey; if it is one, granivore feeding is frequency-independent. The constant v may be considered as a measure of frequency-independent selection (Greenwood, 1985). Values of b and log v can be estimated by linear regression on the log-transformed ratios of eqn 2.

Survivorship of A. turbinata *seeds*

If *F. crenata* seed fall significantly affects *A. turbinata* survivorship, we would expect greater survivorship during the mast year (1995) than during the non-mast years (1996, 1997). However, direct comparison among years is inappropriate, since the abundance of seed predators also varied among years. To overcome this, we calculated two estimates of seed survivorship in each year. The first estimate was derived from the period of *A. turbinata* seed fall prior to *F. crenata* seed fall (no influence of *F. crenata*) and the second period was when both tree species were seeding (effect of *F. crenata*). We estimated the change in survivorship between these two periods using a proportional-hazards model (StatSoft, 1995) and compared the extent of the change among the 3 years.

The proportional-hazards model analysis allows us to incorporate 'censored data' and estimates conditional probabilities of mortality at any given time from a survivorship curve. It is composed of two elements of the survivorship statistics: hazard and hazard ratio. Suppose S is a survivorship curve function. The hazard h is a function of time and defined as:

$$h(t) \equiv -\frac{\mathrm{d}S}{\mathrm{d}t} / S(t) \qquad (3)$$

The hazard shows the 'instantaneous risk' of mortality (Hamajima, 1993; StatSoft, 1995; see also Schupp, 1990). Relative risk of mortality among two survivorship curves can be obtained by the ratio of the two hazards, $h_2(t)/h_1(t)$, where $h_2(t)$ is the hazard function for the period with *F. crenata* seed fall and $h_1(t)$ is the period without. We then compared values of the hazard ratio for each of the 3 years. Only data on seeds removed by rodents were included in the analyses.

Results

Long-term trends in A. turbinata *seed success in relation to seed production*

The seed success of *A. turbinata* varied greatly among the 7 years of the study (coefficient of variation (CV) = 83.8% for seed survival, 88.5% for seedling emergence). However, seed success was not correlated with *A. turbinata* seed production (for seed survival, $r = 0.19$, d.f. = 5, $P = 0.67$; seedling emergence, $r = 0.49$, d.f. = 5, $P = 0.29$) (Fig. 15.1). This suggests that there is little evidence for predator satiation or economies of scale for *A. turbinata* (Janzen, 1971; Norton and Kelly, 1988).

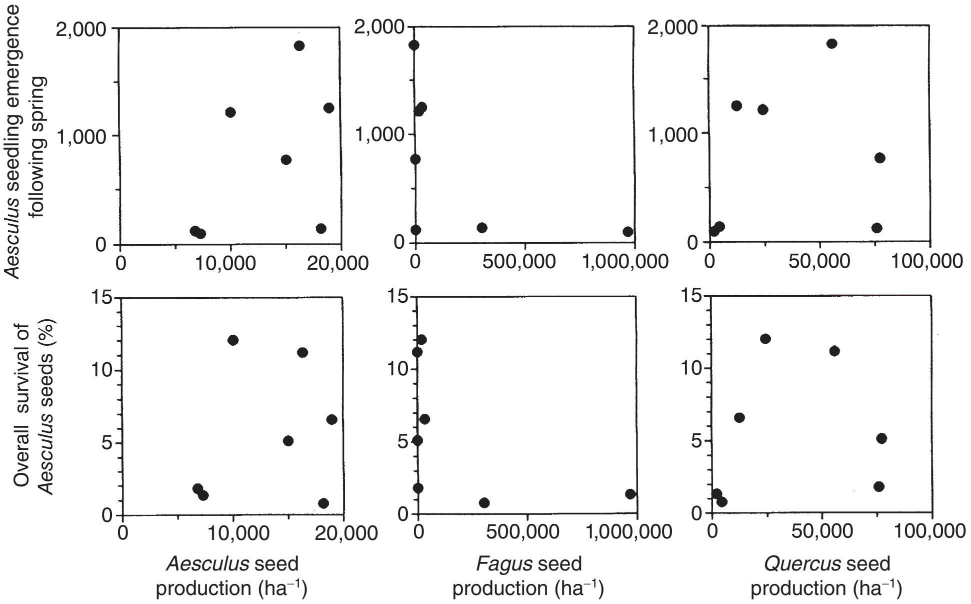

Fig. 15.1. Relationships between seed production of three large-seeded species and overall success of *A. turbinata* seeds. Note that *A. turbinata* seed success was not correlated with its own seed production and was reduced in years of *F. crenata* masting.

Consideration of the availability of the seed of the other tree species provided some support for the indirect effect of *Fagus* masting on *Aesculus* seed survival. *Fagus* exhibited distinct mast years, fruiting only in 1993 (small crop) and 1995 (large crop) during the 7-year monitoring period, while *Q. mongolica* showed an 'alternate bearing' pattern (*sensu* Crawley and Long, 1995) (Fig. 15.2a). Both *A. turbinata* seed survival (< 1.5%) and seedling emergence (< 150 seedlings ha^{-1}) were particularly low during the *F. crenata* mast year and among the lowest in the 7-year observation period (Fig. 15.1). No such trend was observed when *Q. mongolica* massively fruited (Fig. 15.1).

Short-term analysis of seed fate of A. turbinata

Before the seeds of *A. turbinata* established seedlings or were consumed, they experienced various fate pathways through secondary dispersal (Fig. 15.3). Over the 3 years, the initial fate of most seeds was to be placed in a primary cache. Only in 1996 were more seeds

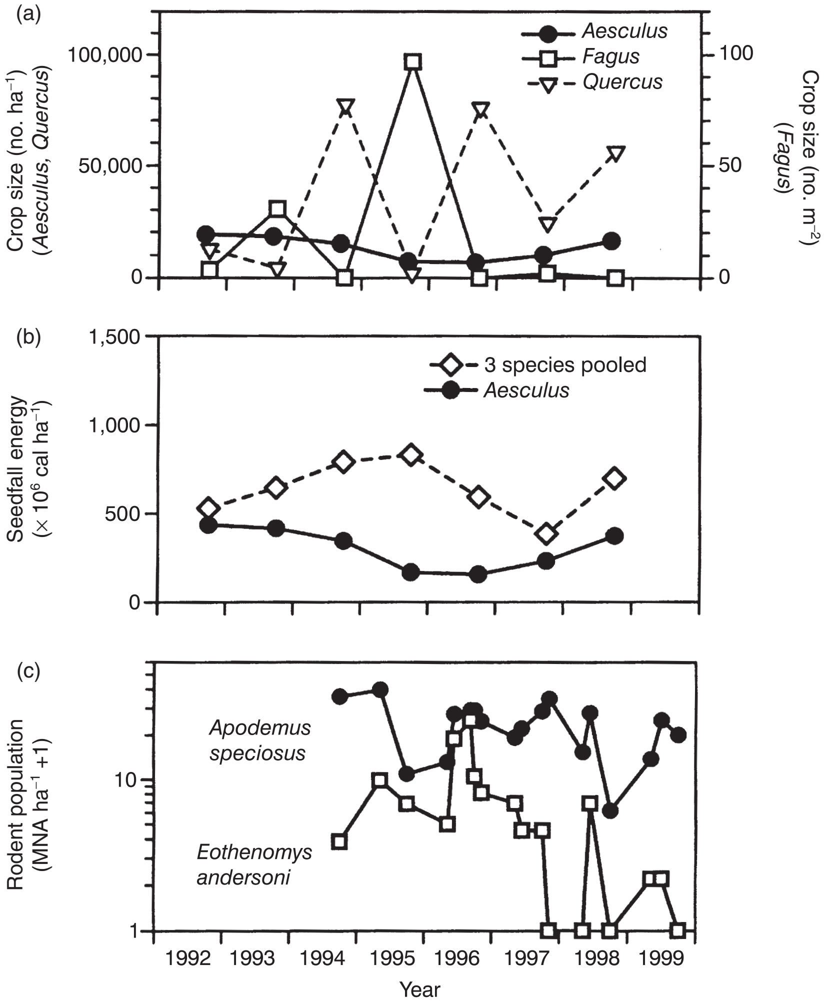

Fig. 15.2. Annual variations in (a) community-wide production of large seeds and (b) their energy values as food resources for consumers, and (c) corresponding numerical responses of rodents.

initially destroyed (60%) than cached (values for 1995 and 1997 were 34% and 17%, respectively). Seed predation was the predominant source of seed mortality, accounting for between 93 and 100% of seed death.

Caches usually contained one seed, though observation in other years indicates that caches with more than ten seeds sometimes occur (Hoshizaki *et al.*, 1997). For most seeds, caching simply delayed subsequent seed predation, as most seeds in primary caches were usually consumed. The ultimate fate of the few seeds that were removed from primary caches and placed into secondary caches was also seed consumption. Although the fate of all seeds was not known, the proportion of seeds that germinated was low, ranging from only 1 to 3%, with over 80% of seeds suffering predation in most years.

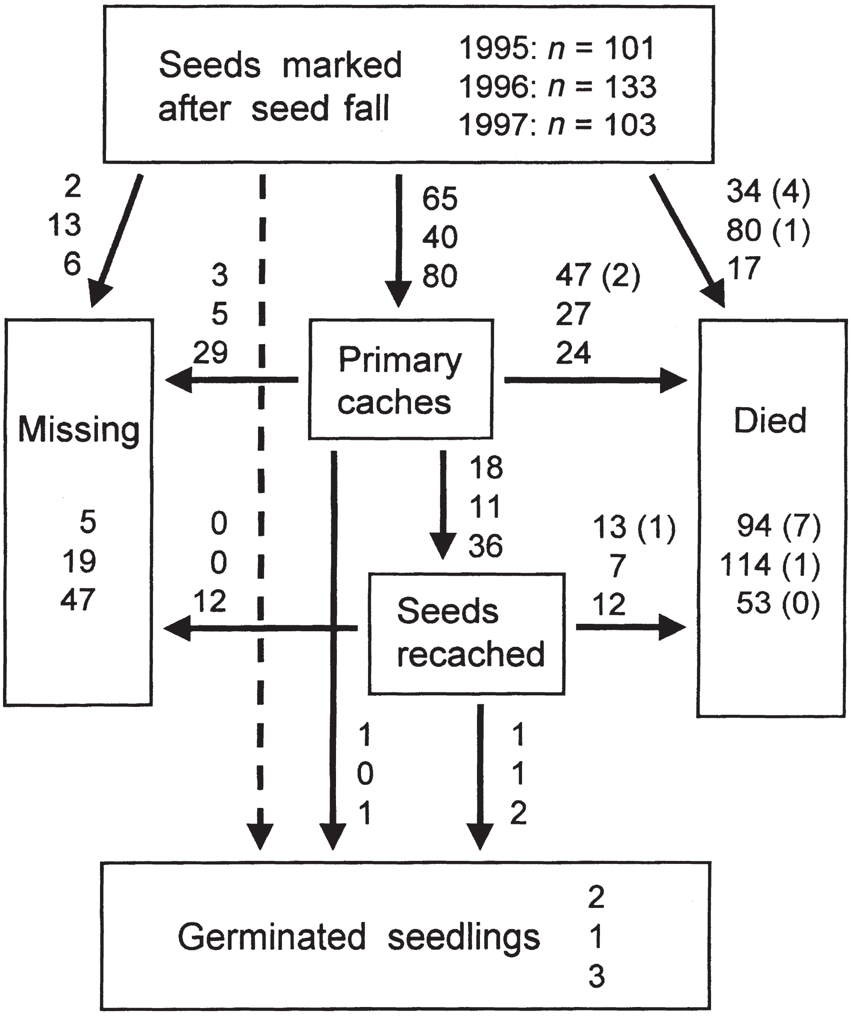

Fig. 15.3. Seed-fate pathways for *Aesculus turbinata*. The three numbers on the side of each arrow indicate transition frequencies for 1995 (top), 1996 (middle) and 1997 (bottom). Because some seeds were moved several times from 'primary cache' to 'seeds recached', summed values for arrows coming into the 'recache' category do not equal the sum of the values for arrows leaving this category. Numbers in parentheses represent the number of seeds that died for reasons other than predation. The broken arrow indicates a pathway which can potentially occur but was never observed during the study.

Seasonal mortality of A. turbinata *seeds*

Levels of seed removal by rodents varied both within the autumn fruiting period and also between years. In 1995, the rate of *A. turbinata* seed removal suddenly decreased in October, despite an abundance of seeds (Fig. 15.4). This coincided with a rapid increase in the density of *F. crenata* seeds and a corresponding increase in *F. crenata* seed removal. This pattern in *A. turbinata* seed predation was not evident in 1996 or 1997 when there was no *F. crenata* masting. Removal of *F. crenata* seed was significantly correlated with its density on the

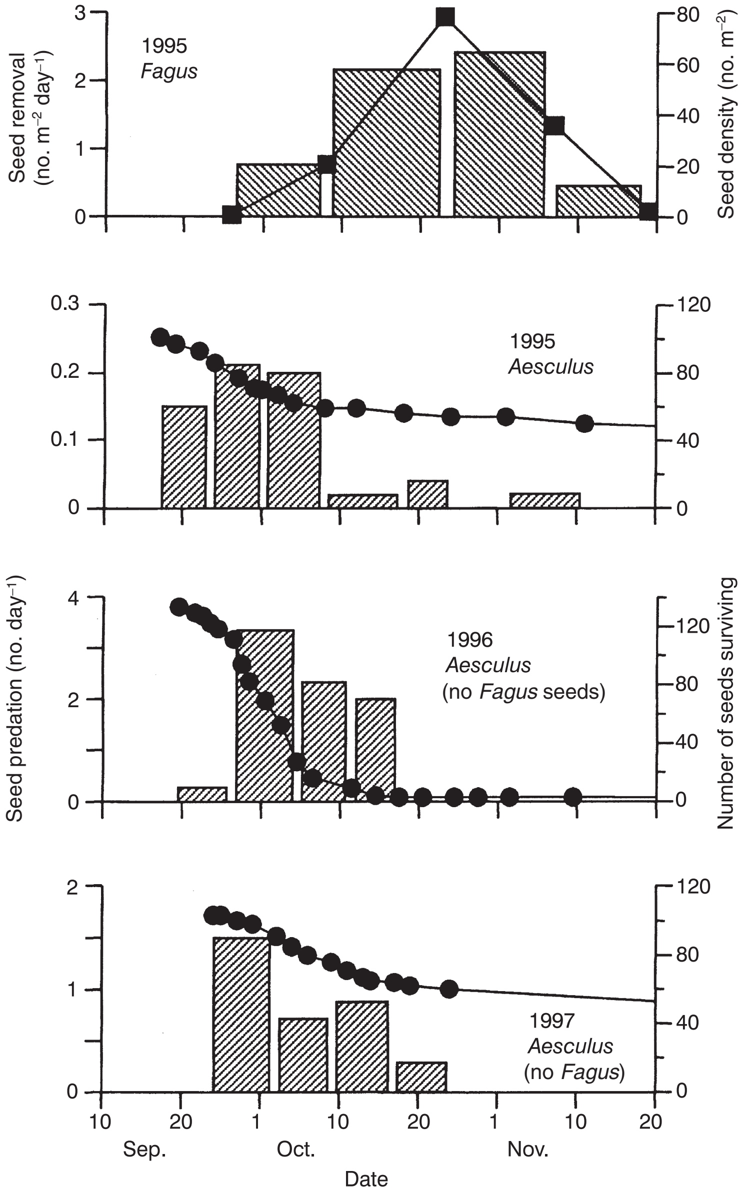

Fig. 15.4. Seasonal changes in seed predation on *Fagus crenata* (top) and on *Aesculus turbinata* (remainder). The rates of predation (bars) and numbers (*A. turbinata*) and density (*F. crenata*) of remaining seeds (lines) are shown. No *F. crenata* seeds were produced in 1996 or 1997.

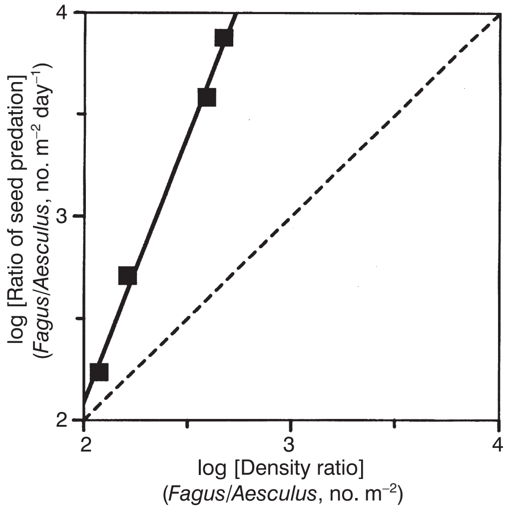

Fig. 15.5. Analysis of frequency dependence in seed predation on *A. turbinata* versus *F. crenata*. A slope of >1 in the regression line indicates stronger preference for *F. crenata* seeds over *A. turbinata* by the predators. Dashed line (slope = 1) shows frequency-independent predation. We obtained a significant regression line with the parameter $b = 3.17$; $r = 0.997$, d.f. = 2, $P = 0.003$.

forest floor ($r^2 = 0.92$, d.f. = 2, $P = 0.04$). Rodents exhibited a strong, consistent preference to *F. crenata* seeds over *A. turbinata* and this preference increased as *F. crenata* seed became more abundant (Fig. 15.5). The results of the proportional-hazards model support the finding that the seasonal change of the seed predation was due to selective consumption of *F. crenata*. The hazard ratio for 1995 was significantly smaller (0.0473, 95% confidence interval 0.0134–0.167) when compared with the ratio in either 1996 (1.426, $\mathrm{CI}_{95\%}$ 0.947–2.14, $P < 0.05$) or 1997 (0.483, $\mathrm{CI}_{95\%}$ 0.202–1.15, $P < 0.05$). This means that the extent of change in the shape of survivorship curve was greatest in 1995 and was associated with the masting period. In spring, patterns of seed survival were reversed and the mortality of *A. turbinata* seeds was higher in the mast year than in 1996 or 1997 (Fig. 15.6). As a result, the overall survivorship of seeds from the mast year was lower than that from non-mast years.

Annual variation in food resources and the numerical response of rodents

Although the species-pooled seed fall abundance varied greatly among years (CV = 142.0%), seed fall energy showed a very small among-year variation (CV = 24.0%), varying by 2.2-fold for max./min. (Fig. 15.2a, b). This was attributable to annual, relatively constant (CV = 38.7%) fruiting of large seeds of *A. turbinata*. However, densities of the two rodent species varied by an order of magnitude. There was no clear relationship between rodent abundance and any of the seed-fall measures, although their populations increased rapidly in the summer following *F. crenata* masting (Fig. 15.2c).

Discussion

Studies of seed dynamics in the Kanumazawa Riparian Research Forest provide considerable insights into the role of community processes influencing plant–granivore interactions. In each of the 3 years studied, the vast majority of *A. turbinata* seeds were removed by rodents. For those seeds whose fate we were able to record, it was evident that rodents destroyed between 90 and 99% of seeds in any 1 year. Nevertheless, although seed predation was particularly intense, between 1% and 5% of seeds successfully germinated from caches to produce seedlings. If seedlings can only

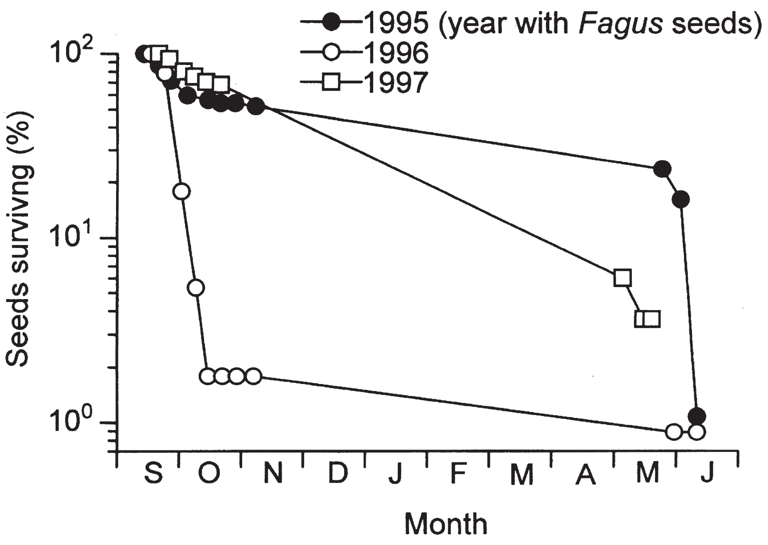

Fig. 15.6. Survivorship curves of *A. turbinata* seeds.

arise from cached seeds, e.g. because seed burial is necessary for successful germination or seeds are transported to suitable microsites, then the net effect of rodent seed removal on plant regeneration will be positive (see Hulme, this volume). Previous research on *A. turbinata* in the Kanumazawa Riparian Research Forest indicates that burial may not be necessary for germination and that seeds are not dispersed to particularly suitable microsites (Hoshizaki *et al.*, 1997, 1999). This suggests that seed dispersal by rodents is not an essential element in the regeneration of *A. turbinata*. Furthermore, there is no guarantee that the small proportion of seeds that actually germinate from caches will subsequently recruit to the adult population. Therefore, the high levels of seed destruction indicate that rodents were acting primarily as seed predators, rather than seed-dispersers.

Although the three dominant tree species show markedly different and uncorrelated fruiting patterns, the resources available to polyphagous rodent seed predators remain, in comparison, relatively constant over the 7 years. We would therefore expect the numerical responses of granivorous rodents to be buffered by the community-wide seed fall. While the temporal dynamics of the rodent populations are variable, there is no clear evidence of them being driven by changes in the seed-fall patterns at either the community or the species level. In such a system, satiation of polyphagous granivores via masting is unlikely to succeed in greater seedling success. Thus, for *A. turbinata* there is no evidence of predator satiation or economies of scale. This situation contrasts with tropical dipterocarp forests, where community-wide synchrony facilitates predator satiation (Curran and Leighton, 2000; Curran and Webb, 2000).

The absence of any clear association between rodent abundance and seed-fall patterns at either the community or the individual species level contrasts with findings where generalist seed consumers respond numerically to increased seed production (Wolff, 1996; Ostfeld and Keesing, 2000). Again, contrary to previous findings (Sork, 1983; Jensen, 1985; Manson *et al.*, 1998), increased seed fall did not increase *A. turbinata* seedling regeneration. These results suggest that, at least in the Kanumazawa Riparian Research Forest, the granivore–plant interaction is not a simple function of the overall abundance of seed resources.

An intuitive assumption of community-wide asynchrony in seed fall is that less-preferred species may benefit from reduced predation during periods when the abundance of a more preferred species increases. The frequency-dependence analysis indicates that rodents strongly prefer smaller *F. crenata* seeds over larger *A. turbinata* seeds. This result is consistent with a field experiment where a choice test was undertaken by providing rodents with both seeds simultaneously (Miguchi, 1996). Since *F. crenata* seeds are rich in per-gram energy and do not contain any saponins or tannins (K. Hoshizaki, unpublished data), this species is expected to be the most palatable among the large-seeded species in our forest. We would therefore expect that there would be less *A. turbinata* seed predation in an *F. crenata* mast year than in a non-mast year. For those seeds whose ultimate fate was known (i.e. not missing), rodents destroyed 91% in the mast year, whereas 99% and 95% were destroyed in the two subsequent non-mast years. This trend is consistent with our expectation, but the significance of the differences among years is questionable. This finding is supported by comparison of the seedling numbers in each of the 3 years. We might expect lower rates of seed predation in the *F. crenata* mast year to facilitate a higher number of *A. turbinata* seedlings. Surprisingly, *A. turbinata* seed survival and seedling emergence were especially low during the *F. crenata* mast period, in complete contrast to our expectations. The highest recorded seedling survival was found in the 1997 non-mast year (K. Hoshizaki, unpublished data). This would suggest that, although *F. crenata* is a highly preferred species, the switching in rodent foraging from *A. turbinata* to *F. crenata* had only a minor effect on subsequent *A. turbinata* seedling regeneration.

Comparison of the daily predation rates (Fig. 15.4) may shed light on this apparent paradox. Rates of *A. turbinata* seed predation in 1995 were an order of magnitude less than in either 1996 or 1997. Although predation rates may have been influenced by the *F. crenata* seed fall (Fig. 15.5), seed predation rates were already low prior to the mast period. These low rates of seed predation appear to reflect both the relatively low levels of *A. turbinata* seed production and the abundance of both rodent species (Fig. 15.2). In 1996, *A. turbinata* seed production was similar to that in 1995 and yet daily rates of *A. turbinata* removal were the highest recorded during the 3 years of study. This coincides with a dramatic increase in the densities of both rodent species in 1996. This may be an indirect effect of the *F. crenata* mast in 1995. By 1997, rodent numbers (especially *E. andersoni*) had declined from the peak in 1996. The result was moderately high rates of seed predation but insufficient to reduce seed numbers as substantially as in 1996. It therefore appears that the patterns of seed predation more or less reflect the change in rodent densities. The abundance of *A. speciosus* in monodominant beech forest of Japan clearly follows the masting cycles of *F. crenata* (Miguchi, 1988). It would therefore be reasonable to expect that the fluctuation in rodent populations reflect, to some extent, the availability of the more preferred species (*F. crenata*) rather than those of the less preferred *A. turbinata*. However, the role of *F. crenata* mast years in the rodent population dynamics cannot be discerned from the data available (Fig. 15.2c). This seems to suggest that there is little evidence for a direct effect of *F. crenata* on these patterns, but the indirect effect through a delayed numerical response in rodent densities cannot be discounted. The considerable annual variation in *A. turbinata* regeneration success contrasts with the relatively constant annual seed fall in this species. This would suggest that other drivers, external to *A. turbinata*, play a role in the regeneration of this species. It is therefore possible that other tree species indirectly affect the regeneration of *A. turbinata* in our multispecies system, though caution must be applied when making generalizations based on only one masting event.

In summary, the value of this research is that it highlights the complexity of the granivore–plant interaction. Clearly, studies based on only 1 year tell us little about the interaction. Even the present 3-year study can only speculate about some of the mechanisms underlying seedling regeneration. Unfortunately, it is evident that the impact of masting needs to be studied over much longer periods. Nevertheless, future studies must assess changes in the focal species as well as other species in the community, not only the granivores but also co-dominant plant species.

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