

15 Influence of Forest Composition on Tree Seed Predation and Rodent Responses: a Comparison of Monodominant and Mixed Temperate Forests in Japan

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Introduction

Plants often suffer heavy mortality in their seed and seedling stages. While some vertebrates play a significant role in seed dispersal, others are predators of seeds and seedlings. In many large-seeded, nut-bearing trees, rodents are responsible both for effective seed dispersal by their vigorous activity of seed hoarding (Vander Wall, 2001), and for early-stage mortality through seed and seedling predation (Crawley, 2000; Kitajima and Fenner, 2000; Hulme and Benkman, 2002). Rodents are pivotal in the regeneration and demography of large-seeded trees.

Conversely, large-seeded trees can affect rodent populations. Large seeds are a high quality food resource (Vander Wall, 2001), but they are not reliable foods for rodents because the trees often exhibit large interannual variations in seed production (Kelly, 1994; Vander Wall, 2001). The large annual variation in seed crops (e.g. masting followed by low seed crops in subsequent years) has a major influence on the population size of predators, such that

the population increases after masting and decreases during low seed-crop years (Wolff, 1996b; Wright *et al.*, 1999; Ostfeld and Keesing, 2000). Variation in rodent numbers may in turn affect seed predation and dispersal in some trees (Vander Wall, 2002; Zhang *et al.*, Chapter 16, this volume). Ingestion of large seeds may have negative effects on rodent physiology; many large seeds, especially *Quercus* acorns and *Aesculus* seeds, contain secondary compounds which operate as a chemical defence against seed predators (e.g. Vander Wall, 2001; Shimada and Saitoh, 2003).

The interaction between large seeds and rodent populations has been intensively studied (e.g. Crawley, 2000; Vander Wall, 2001; Hulme, 2002; Hulme and Kollmann, Chapter 2, this volume, and references therein). The ecological significance of masting is supposedly that synchronous seed production satiates seed predators and so produces a disproportionately large cohort of seedlings following masting (Janzen, 1971; Kelly, 1994). However, because rodents are polyphagous and generalist seed predators (Hulme and

Benkman, 2002), their response to variation in seed crops is likely to be complex in multi-species forest systems (Hoshizaki and Hulme, 2002). In fact, there appears to be considerable variation in rates of pre- and post-dispersal seed predation and subsequent seedling recruitment (Hulme, 1998, 2002). For example, the rate of predation on temperate tree seeds varies with stand locality, habitats, seasons and years (e.g. Willson and Whelan, 1990; Kollmann *et al.*, 1998; Hulme and Borelli, 1999; Hoshizaki and Hulme, 2002; Hulme and Kollmann, Chapter 2, this volume).

An explanation for the variability in seed predation patterns is that indirect interactions within a plant guild in which seed predators are shared may play a role in mixed forest stands (Ostfeld *et al.*, 1996; Hoshizaki and Hulme, 2002). For example, rodents show different responses when the relative abundance of seed species changes (Hulme and Hunt, 1999; Hoshizaki and Hulme, 2002), generating inconsistent rates of seed predation. A number of studies have examined the relationship between abundance of one species of seed and seed predation (e.g. Jensen, 1985; Schupp, 1990; Crawley and Long, 1995), but only a few have attempted to examine predator abundance with reference to community-wide seed availability (Wright *et al.*, 1999; Curran and Webb, 2000; Hoshizaki and Hulme, 2002; Schnurr *et al.*, 2002).

In cool-temperate Japan, the dominant vegetation is beech forests (Nakashizuka, 1987). Forest types differ over relatively small geographical distances but share common component species. Forest stands show marked variation in species composition; there are beech-monodominant stands and mixed stands of large-seeded trees (Nakashizuka and Iida, 1995). Patterns of interaction may vary among stand types. In this chapter, we review the role of rodents on the recruitment of several large-seeded tree species in Japan, with emphasis on the early demography across several years and sites. We explain that the early demography of a single tree population can be affected by the early-stage dynamics of other tree

species within the same forest community. In addition we discuss how the variation in tree community structure and those in seed attributes (e.g. nutritional values) of large-seed producing plants may cause variations in their interaction with rodents. Finally we also attempt to compare case histories for temperate trees and rodents in Japan with findings from similar temperate forests in Western Europe and eastern North America.

Selected Species and Areas

The large-seeded trees

The tree species focused upon in this review are the horsechestnut (*Aesculus turbinata* Blume), beeches (*F. crenata* Blume and *F. japonica* Maxim.) and oaks (*Q. crispula* Blume and *Q. serrata* Thumb. ex Murray). These taxa were chosen because the demography of their seeds and seedlings in relation to community structure is comparatively well understood (e.g. Nakashizuka *et al.*, 1995; Nakashizuka, 2001; Hoshizaki *et al.*, 1997; Homma *et al.*, 1999). Species in warm-temperate, evergreen forests are excluded because less is shown of their interaction with rodents.

Aesculus turbinata (*Hippocastanaceae*) is one of the dominant species in cool-temperate riparian forests, co-occurring with *F. crenata*, *Q. crispula* and several wind-dispersed trees (Table 15.1 in Suzuki *et al.*, 2002). It bears extremely large seeds (21 g fresh weight, 6.2 g dry weight; Hoshizaki *et al.*, 1997). Seeds are carbohydrate- and sugar-rich, but also contain high levels of secondary compounds, especially saponins (Hoshizaki, 1999; Shimada, 2001). Seed dispersal is exclusively by rodents (Isaji and Sugita, 1997). Seeds of *A. turbinata* show hypogeal germination, which enhances seedling resistance to herbivory (Hoshizaki *et al.*, 1997).

In Japan there are two *Fagus* species (*F. crenata* and *F. japonica*) and 15 *Quercus* species. Both the *Fagus* and two *Quercus*

species, *Q. crispula* (synonymous to *Q. mongolica* Fischer var. *grosseserrata* (Blume) Rehd. et Wilis.) and *Q. serrata*, are abundant in cool-temperate old-growth forests. In particular, *F. crenata* is dominant in cool-temperate montane zones and is recognized as a keystone species (see next section). Seeds are removed mainly by rodents (e.g. Miguchi and Maruyama, 1984; Kikuzawa, 1988) and to a lesser extent by birds (passerines and corvids). Fresh weight of the nut or acorn of these Fagaceae species is, in ascending order, 0.16 g for *F. japonica* (S. Taniguchi, unpublished data), 0.20 g for *F. crenata* (Miguchi, 1994), 2.8 g for *Q. serrata* (Iida, 1996) and 3.5 g for *Q. crispula* (Hoshizaki, 1999).

Stand structures

There are two contrasting types of beech forest, differing in both stand structure and geographical distribution. One is a monodominant forest of *F. crenata* and is typically distributed along the Sea of Japan (Japan Sea type). Here, *F. crenata* occupies 70 to nearly 100% of the stand basal area (Table 15.1). In contrast, the Pacific Ocean type is a mixed-species forest in which the dominant species are *F. crenata*, *Q. crispula* (or *Q. serrata*) and in some locations *F. japonica*, distributed along the Pacific Ocean. The dominance of each of these species ranges from 10–40% of the stand basal area (Table 15.1).

Table 15.1. Stand characteristics for seven study sites described in this chapter. Sites with long-term data or with datasets for both rodents and trees in Japan are selected. The seven sites are chosen from cool-temperate old-growth forests. Sites are sorted by location, within the same stand type, from north to south.

Stand type ^{*a} and site	Location	Max. snow depth (m)	Dominant tree species ^{*b}	Rodent investigation	Duration (yr)	Ref. ^{*c}
Japan Sea type beech forest						
Utsai	42°38'N, 140°19'E	≈ 3	<i>F. crenata</i> (> 90)	Habitat	1	6
Lake Towada	40°24'N, 140°53'E	≈ 2	<i>F. crenata</i> (69)	Abundance and habitat	6+	1, 8
Nukumi-daira	37°55'N, 139°41'E	3–4+	<i>F. crenata</i> (99)	Abundance and habitat	11+	2, 7, 8
Buna-daira	36°58'N, 139°16'E	2–2.5	<i>F. crenata</i> (94)	Behaviour	1	11
Riparian mixed forest						
Kanumazawa	39°06'N, 140°52'E	≈ 2	<i>Cercidiphyllum japonicum</i> ^{*d} (26) <i>A. turbinata</i> (19) <i>F. crenata</i> (15) <i>Q. crispula</i> (13)	Abundance	10+	3, 4, 12
Pacific Ocean type beech forest						
Ogawa Forest Reserve	36°56'N, 140°35'E	0–0.5 ^{*e}	<i>Q. serrata</i> (27) <i>F. japonica</i> (21) <i>F. crenata</i> (9)	None	16+	2, 9, 10
Mount Mito	35°45'N, 139°00'E	0–0.3 ^{*e}	<i>F. crenata</i> (36) <i>F. japonica</i> (25)	Behaviour	1	5, 11

*a. See text for definition and references for detailed stand characteristics.

*b. The value in parentheses represents relative basal area (%) for each species in each site.

*c. References: (1) Abe *et al.*, 2001; (2) Homma *et al.*, 1999; (3) Hoshizaki and Hulme, 2002; (4) Hoshizaki *et al.*, 1997; (5) Irie *et al.*, 1998; (6) Kitabatake and Wada, 2001; (7) Miguchi and Maruyama, 1984; (8) Miguchi *et al.*, unpublished; (9) Nakashizuka and Matsumoto, 2002; (10) Shibata *et al.* 2002; (11) Shimano and Masuzawa, 1998; (12) Suzuki *et al.*, 2002.

*d. Seeds of this species are extremely small (0.8 mg), wind-dispersed and not damaged by rodents.

*e. Winter climate is generally dry and snow cover is not continuous throughout winter.

The geographical distribution of the two beech forest types corresponds well to distinct climatic regions with contrasting snowfall regimes (Nakashizuka and Iida, 1995; Homma *et al.*, 1999). The Japan Sea type forests are distributed in areas of humid climate throughout the year and with heavy winter snow (2–4 m or more maximum depth), and the Pacific Ocean type forests are distributed in areas with dry winter and without continuous snow cover throughout the winter.

Riparian forests in cool-temperate Japan are mixtures of various species and occur in both areas along the Pacific Ocean and the Sea of Japan (Sakio, 1997; Suzuki *et al.*, 2002). Riparian stands include *A. turbinata*, *F. crenata*, *Q. crispula* and several wind-dispersed trees and are distinct from the two types of beech forest in Japan (Table 15.1 in Suzuki *et al.*, 2002).

We selected seven study sites, covering both Japan Sea and Pacific Ocean beech forests and a cool-temperate riparian mixed forest (Table 15.1). These sites were chosen to provide data on both seedfall and seed fate within temperate Japan in order to review demographic or behavioural interrelationships between large seeds and rodents, and to examine the response of rodents to inter-annual variation in seed crops in monodominant and mixed forests. The distance between most distant sites (Utsai to Mt Mito) is \approx 800 km.

Post-dispersal seed predators

In the temperate forests in Japan, the most important seed dispersers and predators after seedfall are rodents. Two murid and three microtine species are well documented for their impacts on tree regeneration. The dominant murid rodents in most Japanese temperate forests are *Apodemus speciosus* Temminck and *A. argenteus* Temminck (Miguchi, 1988, 1996a,b). Among the microtines, *Microtus montebelli* Milne-Edwards and/or *Eothenomys andersoni* Thomas occur in most temperate forests except Hokkaido, northern Japan.

These species are usually fewer in number than murid rodents, but can have a substantial negative impact on the tree regeneration (Miguchi, 1988; Kitabatake and Wada, 2001). *Clethrionomys rufocanus* Sundevall is another microtine vole dominant in Hokkaido, but its geographical distribution only overlaps the northernmost populations of *F. crenata*.

Patterns in Seed and Seedling Demography

Negative and positive impacts of rodents on *A. turbinata* regeneration

Seed predation, seedling herbivory and seedling resistance

Seeds of *A. turbinata* are intensively removed (\approx 100%) and scatterhoarded by rodents. Caches usually contain a single seed (Hoshizaki and Hulme, 2002). Rodents typically transport the seeds several times from cache site to cache site. They cache and secondarily disperse seeds within 1–5 m per movement (Isaji and Sugita, 1997). The ultimate fate of each seed is usually to be eaten, but seedling emergence does occur from caches (Hoshizaki *et al.*, 1997; Hoshizaki and Hulme, 2002). A 10-year trend (1992–2001) in overall seed survival (proportion of fallen seeds that emerge) shows a large range of 0.8–27.0% with a mean of 7.7% (K. Hoshizaki, unpublished data). Annual patterns of seed production and seedling emergence are distinct. Based on a 7-year observation period (1992–1999; Hoshizaki and Hulme, 2002), seed production does not vary greatly, with max./min. < 3 (Coefficient of variation (CV) = 38%). On the other hand, seedling emergence ranges from 97 to 1828 seedlings/ha. Seed success therefore varies greatly from year to year (CV = 83%). Seedling emergence for *A. turbinata* varies considerably from year to year but is not seed-limited.

Hoshizaki *et al.* (1997) undertook detailed observations of herbivory and of

the fate of seedlings. Seedlings experienced diverse types of herbivory, including shoot clippings and cotyledon removal by rodents. Many seedlings suffered damage several times and from differing types of herbivory. Seedlings had differing experiences during the first-year growing season. In the case of a large cohort (1248 seedlings/ha) at Kanumazawa riparian forest in 1993, 39% of the seedlings had their cotyledons removed, 40% experienced shoot clipping and many seedlings ($n = 207$) experienced both. When seedlings suffer clipping, they are likely to die; clipping had the strongest effect on seedling mortality, followed by cotyledon removal. In contrast, seedlings not suffering herbivory survived well; in this same cohort the survival rate of intact seedlings reached 74%. Herbivory is therefore the major factor determining seedling demography in this species (Hoshizaki *et al.*, 1997).

Although herbivory decreased seedling survivorship, it never led to 100% mortality. This resistance was associated with the large seed size and hypogeal germination such that the seedlings whose hypogeal cotyledons were intact showed higher survivorship than those whose cotyledons were removed by rodents. Even 1 month after emergence of seedlings of *A. turbinata*, a considerable fraction of seed reserves remains in hypogeal cotyledons (Fig. 15.1A). By drawing on these resources, seedlings were able to produce a callus and resprout after the shoot has been clipped (Fig. 15.1B). Resprouting corresponded significantly to retention of hypogeal cotyledons (Hoshizaki *et al.*, 1997). Since removal of hypogeal cotyledons had no effect on seedling size, these results indicate that the large reserve resources in cotyledons act to reduce the mortality risks from herbivory, as has been found for tropical trees (Forget, 1992; Harms and Dalling, 1997; Kitajima and Fenner, 2000). Regeneration in *A. turbinata* is therefore herbivore-limited (*sensu* Crawley and Long, 1995; Crawley, 2000). The seedlings, however, show high resistance associated with the large seed size, mitigating to some extent the negative impact of rodents on the survival of seedlings (Hoshizaki *et al.*, 1997).

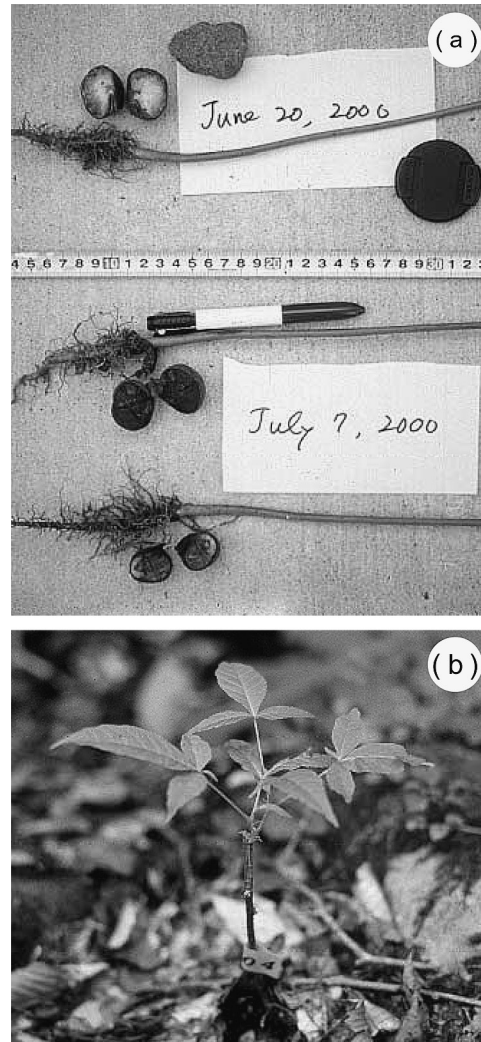


Fig. 15.1. The role of seed reserves stored in hypogeal cotyledons in *Aesculus turbinata* seedlings. (A) A large amount of reserves is stored in hypogeal cotyledons after seedling emergence. Seedlings 3 weeks and 5 weeks after emergence are shown, when their shoots no longer elongate. (B) A seedling resprouted after shoot clipping by rodents. The reserves in hypogeal cotyledons play a significant role on the resprouting (Hoshizaki *et al.*, 1997). Photo by: K. Hoshizaki.

Demographic consequence of seed dispersal by rodents

The role of rodent caching on regeneration can be evaluated from the survival and

growth of seedlings (e.g. Nakashizuka *et al.*, 1995). In Japan, dispersal effectiveness has been evaluated by these means in *A. turbinata*, *Q. serrata* and several other species (Nakashizuka *et al.*, 1995; Iida, 1996; Hoshizaki *et al.*, 1997, 1999). In *A. turbinata*, three hypotheses concerning the selective significance of seed dispersal have been tested, namely the colonization, escape, and directed-dispersal hypotheses (Howe and Smallwood, 1982). Hoshizaki *et al.* (1997; 1999) have proposed that the colonization and escape hypotheses apply to *A. turbinata*, with more support for the former.

The spatial distribution patterns of fallen seeds and emergent seedlings are distinct. Seedlings are widely distributed, but fallen seeds are highly aggregated beneath the canopy of mother trees (Hoshizaki *et al.*, 1997). Rodents play a significant role in enlarging the seed–seedling shadow by gathering seeds and transporting them to cache sites; the tail of the seed–seedling shadow distribution reaches up to 42–115 m from the parent tree (12.2–44.7 m for the means of 3 years; Hoshizaki *et al.*, 1999). These values are comparable to other large-seeded *Fagaceae* (Jensen and Nielsen, 1986; Miguchi, 1994; Iida, 1996). Since seedlings of *A. turbinata* showed higher rates of survival and growth in sites with higher light levels, such as canopy gaps, these results support the colonization hypothesis. Similar effects were found for *Q. serrata* (Nakashizuka *et al.*, 1995; Iida, 1996). Second, seedling survival rate was slightly density-dependent; in sites with a sufficiently low density of seedlings the survival rate was higher, supporting the escape hypothesis (Hoshizaki *et al.*, 1997). However, its role in seedling regeneration may be weak, since seedling herbivory is not density-dependent and the light level was a more important determinant of seedling survival than the seedling density (Hoshizaki *et al.*, 1997, 1999). These results suggest that the escape hypothesis is less important for *A. turbinata*.

At the other extreme, the seed shadow of *A. turbinata* cannot extend beyond the canopy in the absence of rodents. In autumn 2002, the density of *A. speciosus* was

unusually sparse (≈ 2 animals/ha). The spatial distribution of *A. turbinata* seedlings in 2003 was highly aggregated; $\approx 85\%$ of the emerging seedlings were beneath the canopy of *A. turbinata*, even though the seedling density was much higher (≈ 3700 seedlings/ha) than in other years of study (K. Hoshizaki, unpublished data). Although *E. andersoni* was relatively abundant in this period (≈ 27 animals/ha), they are larderhoarders and have smaller home range than *A. speciosus* (Miguchi, 1996a). These results suggest that *E. andersoni* plays only a minor role, if any, on seed-shadow enlargement. Aggregation of seedlings beneath conspecifics leads to an increase in attacks on roots and shoot by *E. andersoni*, and a high rate of infestation by shoot-mining moth larvae (*Hepialidae* sp.), whose density is low in normal years. When the density of this minor herbivore is high, it reduces the performance of second-year seedlings by damaging the apical shoot (K. Hoshizaki, unpublished data). Thus, *A. turbinata* cannot regenerate successfully without seed-dispersing rodents, especially *A. speciosus*. Although rodents have a strong negative impact on *A. turbinata*, the net effect is positive and the interaction between them may be mutualistic; the size of the rodent populations is important, because too few or too many rodents can reduce regeneration of *A. turbinata*.

Geographical variation in *F. crenata* nut predation

Several explanations have been proposed for the geographical variation in beech dominance between the Japan Sea and Pacific Ocean types of beech stand. Homma *et al.* (1999) summarized these explanations and set out the following four hypotheses concerning beech regeneration:

1. Nut production of *F. crenata* is lower in regions where it is less dominant (the production hypothesis);
2. Pre-dispersal predation is severe in regions of lower snowfall (pre-dispersal predation hypothesis);

3. Because the snow pack constrains rodent activity for a longer period, post-dispersal nut predation is less severe in snow-rich regions (post-dispersal predation hypothesis);

4. A relatively dry winter climate in regions of lower snowfall may cause higher mortality of nuts by desiccation (desiccation hypothesis).

Homma *et al.* (1999) tested these hypotheses by simultaneously monitoring the early demography of *F. crenata* for a mast event in 1993, when this species fruited synchronously across its range. They monitored the density of *F. crenata* nuts after nutfall and the following spring in 15 locations in *F. crenata* forests, covering the distribution range of *F. crenata* forests. Production of *F. crenata* nuts varied among the locations but was not correlated with snow depth (no support for the production hypothesis). The proportion of viable nuts, however, was correlated with snow depth, and the proportion of nuts damaged by invertebrates was negatively correlated with snow depth. These results support the pre-dispersal predation hypothesis. Seedling emergence among the locations showed a contrasting pattern. The number of nuts surviving in the following spring was ≈ 120 nuts/m² at the heavy snow (> 2 m deep) sites, but was only 17 nuts/m² at sites having less snow (< 1 m deep). The seedling emergence ratio (density of emerged seedlings to that for the preceding nutfall) was positively correlated with snow depth; at deep snow sites, 15–50% of fallen nuts produced seedlings, but only 0–20% did so at sites with less snow. These results partly support the post-dispersal predation hypothesis. Nut mortality from causes other than vertebrate predation varied widely (0–58%) among sites, but was dominated by microbial decay. Death from desiccation was not observed in most of the studied sites. Maruta *et al.* (1997) also reports low nut mortality from desiccation in a Pacific Ocean type beech forest, Mount Fuji. These findings suggest that desiccation may not be critical for *F. crenata* nuts even under dry winter condition in the Pacific Ocean type forests. Regeneration of *F. crenata*, therefore,

varies geographically and this variation is correlated with snow-depth, and pre- and post-dispersal predation are major factors relating to the variation.

The clear contrast in snowfall regime between the stand types (especially for maximum snow depth and duration of snow cover) may be a key to understanding the variation in *F. crenata* regeneration. Shimano and Masuzawa (1998) studied *F. crenata* nut predation in a Pacific Ocean type forest and a Japan-Sea type *F. crenata* forest (Mount Mito and Buna-daira, respectively; Table 15.1) and found marked difference in nut removal rates between the forests (100% in Mount Mito vs. 30% in Buna-daira). However, in Mount Mito, rodents did not find nuts which were wrapped in a combination of a paper envelope (to remove visibility) and a zippered polyethylene bag (to reduce smell). The detection rate was modest when the nuts were bagged by either the envelope or the polyethylene bag. These results imply that thick snow accumulation could interfere with rodent feeding activity and ability to detect nuts, through reduction in olfactory and visual cues, leading to higher nut survival in snow-rich regions.

Response of Rodents to Variable Seed Resource

Assumptions for predator satiation

The ecological significance of masting is generally taken to be that synchronous seed production leads to satiation of seed predators, both specialists and generalists, resulting in a disproportionately large cohort of seedlings. Additionally, in inter-mast years seed production is often much reduced, reducing the density of seed predators (Kelly, 1994; Ostfeld and Keesing, 2000; and references therein). Several assumptions are involved in these scenarios. However, these patterns may not hold in complex communities, such as multi-species mixed forests with generalist seed predators, for the following reasons.

First, the abundance of seed predators decreases during periods of reduced resources. However, this may be problematic when the predators are generalist, and other tree species may influence the predator population between mast events. For example, we can expect that rodents maintain a high population level even in inter-mast years by consuming alternative resources (Hoshizaki and Hulme, 2002).

Second, seed predators are assumed to respond to *single* species of seed of a mast-fruiting plant. However, the foraging pattern of generalist predators depends on resource availability (e.g. Hulme and Hunt, 1999). Vander Wall (2002) found that synchronous fruiting of sympatric *Pinus* species facilitates seed dispersal via active caching of seeds by rodents, resulting in increased dispersal distance. Furthermore, most studies have evaluated seed supply to predators by the total number of fallen seeds (e.g. Pucek *et al.*, 1993; Choquenot and Ruscoe, 2000). This may be an inappropriate measure if the seedfall of different species is not equivalent (Schnurr *et al.*, 2002). Although seeds vary in nutritional value and in secondary compounds (Grodziński and Sawicka-Kapusta, 1970; Shimada, 2001; Vander Wall, 2001), differences in the resource quality of the mast to predators has received little quantitative attention.

Finally, the numerical response of mammalian seed-consumers often shows a time lag after masting events (Curran and Leighton, 2000; Ostfeld and Keesing, 2000). This point is important for rodents, because a numerical response of rodents in the spring following a mast crop could increase their seedling predation, and the beneficial effect of masting should therefore be tested using both seed and seedling censuses (Hoshizaki *et al.*, 1997; Hoshizaki and Hulme, 2002).

Annual seed production and synchrony

In evaluating patterns of annual seed production, the degree of among-species synchrony is important. Here, we selected

patterns in annual production and synchrony of large-seeded trees in three different forest stand types: a Japan Sea (Nukumi-daira), a Pacific Ocean (Ogawa Forest Reserve) and a riparian mixed forest (Kanumazawa). In Nukumi-daira, the pattern is the simplest and clearest. During 11 years of monitoring, *F. crenata* fruited in 7 years, with three very good crops (1990, 1993 and 1999) and four bad crops (1992, 1997, 1999 and 2000). The nut supply is highly pulsed in this monodominant forest (Fig. 15.2A).

In mixed-species forests (Kanumazawa and Ogawa), the patterns of among-year variation in the community-wide seed abundance are more complex (Fig. 15.2B). In Kanumazawa, *F. crenata* and *Q. crispula* showed large year-to-year variation in seed production. Masting of *F. crenata* occurred in 1993 (small crop), 1995 (large) and 2000 (moderate), and *Q. crispula* showed an 'alternate bearing' pattern (*sensu* Crawley and Long, 1995). The annual seed production of *A. turbinata* was less variable (CV = 45%, 1992–2000). The patterns of annual seed production among the three species were not synchronised (Fig. 15.2B), as reported in England (Gurnell, 1993) and California (Koenig *et al.*, 1994). Since *A. turbinata* seeds are much larger in size and have similar energy per gram to *Q. crispula*, the community-wide seed energy varied relatively little from year to year (Hoshizaki and Hulme, 2002), except for 1999. In Ogawa, seed production of major component species have been monitored since 1987 (e.g. Nakashizuka and Matsumoto, 2002). Shibata *et al.* (2002) has analysed seed crop patterns over a 9 year period for 16 tree species. Many species shared mast years, with a high degree of synchrony among species (in 1988, 1993 and 1995), but *Q. serrata* and *Q. crispula* showed little between-year variability (Shibata *et al.*, 2002). The annual fruiting patterns differed among major large-seeded trees in Ogawa forest (*F. crenata*, *F. japonica*, *Q. serrata* and *Q. crispula*). Both *Fagus* species showed large inter-annual fluctuations in nut production, but their fruiting was not correlated with each other. In contrast, the fruiting patterns of *Quercus*

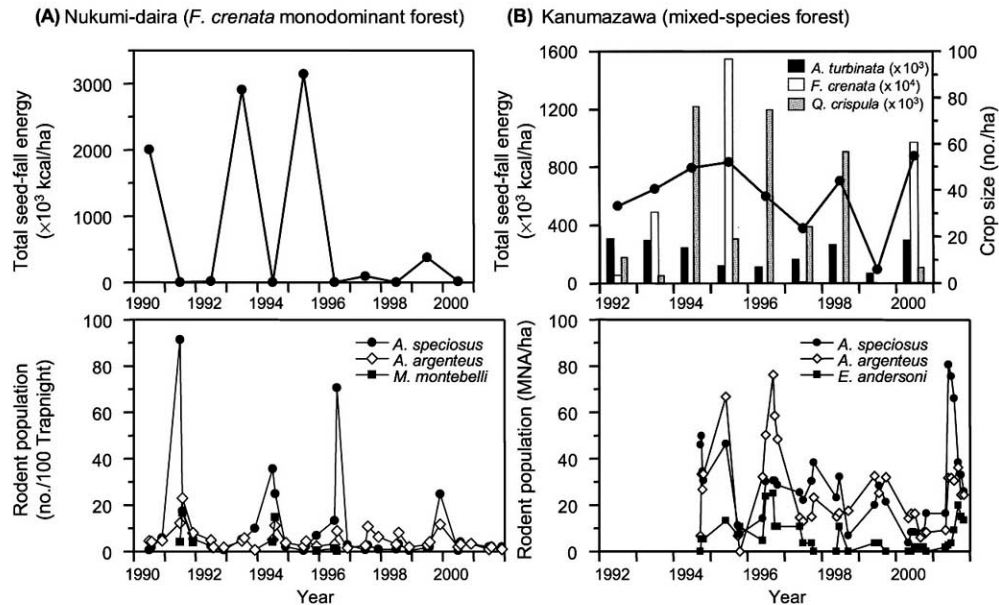


Fig. 15.2. Annual variations in seed resources and rodent numerical responses in (A) monodominant forest of *Fagus crenata* (Nukumi-daira) and (B) a mixed-species forest (Kanumazawa). Seed resources are represented by numbers of fallen seeds (bars) and community-wide seed-fall energy (lines). Rodent populations are monitored using Sherman live traps placed in a matrix. Rodent abundance was represented by number of animals per 100 trapnights (Nukumi-daira) or minimum number of animals alive (MNA; Kanumazawa). Data sources: A) Miguchi (1995, 1996a, and unpublished); (B) Hoshizaki and Hulme (2002) and K. Hoshizaki (unpublished).

spp. were less variable and more synchronized than *Fagus* spp. Thus, community-wide seed availability in mixed-species forests is less variable than in monodominant forest, but includes a pulse of nutritious nuts of *Fagus* spp. In North America, acorn production of *Quercus* spp. is not highly synchronized among species (Koenig *et al.*, 1994; Schnurr *et al.*, 2002), implying a less variable community-wide seed resource between different years.

Numerical response after masting

We examine the numerical response of rodents using data for Japan Sea type beech stands (Nukumi-daira and Lake Towada) and a mixed-species stand (Kanumazawa). Although the seed-resource availability differs between the Japan Sea and the mixed-species stands, rodent numbers in

these forests show similar patterns of response (Fig. 15.2). In *F. crenata* monodominant forests, rodent abundance clearly follows the masting cycle of *F. crenata*; in Nukumi-daira, the number of rodents, especially for *A. speciosus*, increases dramatically every spring after mast events, but such high densities are maintained for only a few months (Fig. 15.2A). *M. montebelli*, which usually inhabits pastures and cultivated fields, is found in beech forests only in the year following *F. crenata* mast events. Similar patterns are observed in Lake Towada (M. Abe *et al.*, unpublished). Jensen (1982) also documents clear eruptions of the *Clethrionomys glareolus* population after masting in a *Fagus sylvatica* monodominant forest in Denmark. Miguchi (1988) investigated changes in the population structure of rodents in relation to masting at Nukumi-daira, and found that recruitment of young individuals makes a large contribution to the

population-increase phase. Thus, the large pulse of *Fagus* mast causes large fluctuations in rodent populations in mono-dominant forests, with a high degree of predictability.

Population fluctuations also occur in mixed forests but are not easy to explain. In Kanumazawa, rodent populations showed large fluctuations from year to year, as in Nukumi-daira, but maintained on average greater total biomass (Miguchi, 1988; K. Hoshizaki, unpublished). Similar results have been reported for *Nothofagus*-monodominant stands and *Podocarpus*-hardwood-mixed stands in New Zealand (Choquenot and Ruscoe, 2000). These findings support the idea that rodent abundance should be buffered in mixed forests, because of asynchronous seed production (Hoshizaki and Hulme, 2002). Nevertheless, the effects of *F. crenata* masting are clear in Kanumazawa. The amplitude of density fluctuations in rodent populations varied from year to year, and there were distinct density peaks after *F. crenata* masting, especially in summer 2001 (Fig. 15.2b). In North America, patterns of population increase differ between species; *Peromyscus* species numerically respond to red oak (*Q. rubra*) masting, but population of *C. gapperi* is correlated with masting of *Acer rubrum* and *Tsuga canadensis* and not with red oak (Schnurr *et al.*, 2002). There appear to be species-specific responses to seed crops, resulting in complex ecological patterns in mixed forests.

Thus in addition to the effect of less snow cover, the greater seed-predation pressure in Pacific Ocean beech forests (Homma *et al.*, 1999) may also be associated with higher rodent densities, which may be buffered by another seed pulse of *Q. crispula* and/or *F. japonica* in non-mast years of *F. crenata*. In fact, fruiting of *F. crenata* and *F. japonica* is not synchronized (Shibata *et al.*, 2002), but this idea should nevertheless be tested empirically.

In Nukumi-daira and Kanumazawa, the peak rodent density did not persist for long. Densities, especially for *A. speciosus* and microtine species, decrease rapidly within the year. Several authors have also reported

population declines in generalist seed predators after the mast is depleted (Miguchi, 1988; Wright *et al.*, 1999; Ostfeld and Keesing, 2000). However, the population fluctuation in Kanumazawa cannot be fully explained under an assumption that rodents similarly respond to different seed species, since the rodent fluctuations showed much larger variation between years than the large-seed availability and because higher total seedfall energy in the preceding autumn does not always lead to a subsequent population increase of rodents in some years (e.g. 1998 seedfall) and vice versa (e.g. 1996 seedfall) (Fig. 15.2B). In 1996, *A. turbinata* made larger contribution to the total seedfall energy than *Q. crispula*, and the reverse is true in 1998. *F. crenata* did not fruit in those years. This suggests that the response of rodent populations to seed supply is not a simple function of total seedfall energy and, in addition, that larger seed crop of *Q. crispula* on the rodent population is unclear (Miguchi, 1996b). Jensen (1982) argues that one factor stimulating the rapid increase in the *C. glareolus* population is seed quality, since *F. sylvatica* seeds have the highest energy content of the tree seeds there. The pattern in mixed stands implies different mechanisms than simple numerical response, such as changes in reproductive schedule (Wolff, 1996b) and winter survival (Jensen, 1982; Wolff, 1996a). The reproductive schedule of Japanese rodents differs from that in Europe and North America. In Europe and North America, rodents often begin to reproduce in late winter following masting (Jensen, 1982; Pucek *et al.*, 1993; Wolff, 1996b). However, winter reproduction has not been observed in Nukumi-daira or Kanumazawa even after good seed-crops (Miguchi, 1988; K. Hoshizaki, unpublished data).

Influence of *F. crenata* mast on *A. turbinata* with shared predators

Since *A. turbinata* shares seed predators with *F. crenata*, its regeneration may be affected indirectly by *F. crenata* masting.

The discordant annual patterns in seeds and seedlings found in a 7-year study of *A. turbinata* seed dynamics in Kanumazawa (Hoshizaki and Hulme, 2002) strongly suggest that the regeneration cannot be explained solely by direct interaction between *A. turbinata* and its seed predators and dispersers.

The overall seed survival rate in *A. turbinata* was not correlated with its seed production, but tended to be low in mast years of *F. crenata* and were unaffected by *Q. crispula* seed crops. This long-term trend suggest that there is little evidence for predator satiation by *A. turbinata*, and also shows that *A. turbinata* seed survival may be indirectly affected via rodent responses to *F. crenata* masting. However, the mechanisms of these indirect effects are complex. In the 1995 *F. crenata* mast year and the 2 subsequent non-mast years, Hoshizaki and Hulme (2002) followed the fate of *A. turbinata* seeds almost daily, and examined whether the rate of *A. turbinata* seed predation is affected by the nutfall pattern of *F. crenata*. The rate of predation on *A. turbinata* seeds varied both within the fruiting period and from year to year. Rodents clearly responded in a frequency-dependent manner to *F. crenata* nutfalls and ignored *A. turbinata* caches. This indicates that rodents preferentially shifted their diet from *A. turbinata* seeds to *F. crenata* nuts (Hoshizaki and Hulme, 2002). However, this change in seed predation played only a minor role in the overall seed demography of *A. turbinata*, because the seeds suffered high mortality just before seedling emergence resulting in lower overall survival in the *F. crenata* mast year than in the other 2 years. The reason for the change in predation on *A. turbinata* seeds in spring remains unknown. Nevertheless, the data have strong implications for the mechanisms underlying apparently inconsistent seed predation patterns; rodent foraging can vary in response to community-wide resource availability, even on a month-to-month basis.

The *A. turbinata*–*F. crenata* interaction in Kanumazawa seems to contrast with the seed dynamics in *F. crenata* monodominant forests. In *F. crenata*

monodominant forests, rodents consume *F. crenata* nuts in a density-dependent manner (direct interaction) in mast years (Abe *et al.*, 2001; Tomita *et al.*, 2002) and thus predator satiation (direct interactions) may be expected (see also Schupp, 1992). It is suggestive that the direct effects on seed survival was apparent in *F. crenata* monodominant forests, but not in mixed forest (Kanumazawa) where indirect effects must be taken into account.

Seed quality and rodent physiology

Why does the response of rodents to resource fluctuation vary with seed species? Differences in seed nutritional composition may be a key factor associated with the population response, since seed nutrition also affects the physiological condition of individual rodents. In particular, levels of lipids have a major influence on seed preference and energy assimilation (Grodziński and Sawicka-Kapusta, 1970; Smith and Follmer, 1972; Smallwood and Peters, 1986; Stapanian, 1986). For instance, Smith and Follmer (1972) found that grey squirrels prefer lipid-rich (20% dry weight) *Q. shumardii* acorns over lipid-poor (4.6% dry weight) *Q. alba* acorns, and that they have a higher rate of energy assimilation of *Q. shumardii* acorns. The predictable numerical response found in Nukumi-daira and the clear preference for *F. crenata* nuts over *A. turbinata* in Kanumazawa (Hoshizaki and Hulme, 2002) suggest that, among *F. crenata*, *Q. crispula* and *A. turbinata*, lipid-rich *F. crenata* nuts are the highest quality food resource for rodents.

Secondary compounds in seeds, such as tannins, can have deterrent effects on rodents (chemical defence). Tannins are known to reduce digestibility of seeds and body mass of rodents (Vander Wall, 2001 and references therein), and in some cases even to cause mortality (Shimada and Saitoh, 2003). Vander Wall (2001) compiled the nutritional values of acorns of various *Quercus* in North America, and noted that black-oak acorns (species of subgenus

Erythrobalanus) have higher levels of both lipids and tannins than white-oak acorns (subgenus *Lepidbalanus*). Some rodent species cannot maintain their body mass when fed tannin-rich acorns of black oaks (Briggs and Smith, 1989). In contrast, white-oak acorns serve as high-quality foods for rodents, because rodent populations increase rapidly after masting of these oak species (e.g. Wolff, 1996b).

In temperate Japan, evidence for a rodent population increase after masting of *Quercus* acorns is not clear (Miguchi, 1996b; Hoshizaki and Hulme, 2002). The reason why masting of Japanese *Quercus* acorns does not lead to an increase in rodent populations may lie in the chemical properties of the seeds. Recently, Shimada and Saitoh (2003) studied the physiology of captive *A. speciosus* individuals fed with *Q. crispula* and *Q. serrata* acorns. They found that: (i) feeding on acorn alone leads to a significant decrease in rodent body mass and daily intake for both acorn species, sometimes resulting in death; (ii) *Q. crispula* acorns, which contains about three times the levels (11.7% dry weight) of tannins as *Q. serrata*, have stronger effects, causing mortality or severe decrease in body mass; and (iii) a tannin-free formula diet that is otherwise similar to natural acorns causes little change in body weight. These results strongly suggest that tannins in *Q. crispula* and *Q. serrata* acorns reduce the quality of these large, carbohydrate-rich seeds. Hoshizaki (1999) made a similar speculation to explain the discordance between the large fluctuation in rodent abundance and the small variation in energy availability (mostly owing to *A. turbinata* seeds) in Kanumazawa (Fig. 15.2B); for rodents, the quality of *A. turbinata* seeds appears to be lower because of the effects of saponins, though this hypothesis needs further experimental testing. Evidently seed attributes, especially lipid contents and chemical defence, may be important in the mechanisms underlying the complex patterns of rodent abundance (e.g. Stapanian, 1986; see also Hoshizaki and Hulme, 2002) in relation to variable seed production in mixed-species forests.

Conclusions

Rodents have significant impacts on tree regeneration. In particular, granivorous, seed-dispersing mice may have a large influence on early demography of trees. Studies on *A. turbinata* regeneration illustrate that seeds and seedlings suffer large impacts, through seed predation and seedling herbivory. The seedling resistance to herbivory and seed dispersal by rodents, particularly *Apodemus speciosus*, are effective to mitigate these negative effects. However, the effects vary from year to year and between forests with differing stand structures. In temperate Japan, forests differing in structure, but with the same major species, occur in a relatively narrow geographic area. By comparing results of demographic studies having similar methodology between *F. crenata* monodominant forests and multi-species forests, differences in the patterns of interactions between large seeds and rodents are discernible. In monodominant forests, the patterns of regeneration and rodent fluctuation may be predictable, because the annual resource supply is highly pulsed. In contrast, studies of indirect interactions among *F. crenata*, *A. turbinata* and rodents demonstrate that the patterns of interactions are much more complex in multi-species forests. Important points in understanding the regeneration dynamics of multi-species systems are:

1. The degree of asynchrony in seed production among species and years;
2. The inter-species variation in seed quality, which includes energy content and deterrent effects of secondary compounds;
3. Rodents' foraging response to seeds with different quality;
4. The species-specific response of rodents to seed production.

Levels of pre-dispersal seed predation may also be important, which should be reviewed elsewhere. Empirical studies on tree-rodent ecology in multi-species system remain sparse. Further accumulation of data on the dynamics in multi-species forests would increase our understanding of the mechanisms of regeneration and

co-existence and of patterns in tree–rodent interactions in temperate forests (Nakashizuka, 2001), and perhaps in more species-rich systems such as tropical forests.

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