

SYNCHRONIZED ANNUAL SEED PRODUCTION BY 16 PRINCIPAL TREE SPECIES IN A TEMPERATE DECIDUOUS FOREST, JAPAN

MITSUE SHIBATA,^{1,2,6} HIROSHI TANAKA,¹ SHIGEO IIDA,¹ SHIN ABE,³ TAKASHI MASAKI,⁴ KAORU NIYAMA,¹
AND TOHRU NAKASHIZUKA⁵

¹Forestry and Forest Products Research Institute, P.O. Box 16, Tsukuba Norin Kenkyu Danchi, Ibaraki 305-8687, Japan

²Graduate School of Bioagricultural Science, Nagoya University, Nagoya 464-8601, Japan

³Forestry and Forest Products Research Institute, Hokkaido Research Center, Sapporo 062-8516, Japan

⁴Forestry and Forest Products Research Institute, Tohoku Research Center, Morioka 020-0123, Japan

⁵Research Institute for Humanity and Nature, Kitashirakawa Oiwakecho, Kyoto 606-8502, Japan

Abstract. To investigate synchronized annual fluctuation of seed production and its advantage for regeneration at the community level, for nine years (1987–1995) we monitored the flowering, seed production, and seedling emergence of the 16 principal tree species in a temperate deciduous forest, Ogawa Forest Reserve, in central Japan.

We found that the species with higher synchronized flowering within a population had larger fluctuation of annual seed production at the population level. The coefficient of concordance of flowering and the coefficient of variation of annual seed production were continuously distributed among species, making it difficult to distinguish masting from nonmasting species. The annual seed production patterns of the 16 species were classified, by cluster analysis, into groups that synchronize their fluctuation of annual seed production. This analysis showed a highly synchronized annual seed production, not only among congeneric species, but also among species of different families.

Although our results have some insufficiency of statistical significance, they did show that predator satiation, both in a population and a guild, effectively operated for many species to enhance seed survival at the pre-dispersal stage. They also showed that pollination efficiency was likely to be operating at the population level for half of the wind-pollinating species. However, generalist predator satiation at the postdispersal seed stage may not operate in a simple, detectable manner in this species-rich forest community.

It is highly probable that there are combined effects of several factors: limited weather triggers for flowering, common flowering physiology among taxonomically related species, and the ecological advantages at the population and guild levels, may cause multiple species to have synchronized fluctuation patterns of seed production.

Key words: Japan; masting; Ogawa Forest Reserve; pollination efficiency; predator satiation; seed production; synchrony; temperate deciduous forest.

INTRODUCTION

The synchronized intermittent production of seeds by tree populations, called masting (Kelly 1994), has been reported for many tree populations (see Herrera et al. 1998). Does the synchronized annual seed production have any advantages for regeneration? Several hypotheses, e.g., pollination efficiency (wind pollination), predator satiation, animal pollination, animal dispersal, and environment prediction, have been proposed with regard to the selective advantages of masting (see review in Kelly 1994). These hypotheses are categorized as “economy of scale” hypotheses, in which larger reproductive effort is more efficient, favoring an occasional large effort rather than regular, smaller ones (Norton and Kelly 1988).

Among these hypotheses, “pollination efficiency” and “predator satiation” have strongly explained the

masting of single species, at the population level (Kelly 1994). The pollination efficiency hypothesis has explained mainly masting in wind-pollinated species (Nilsson and Wästljung 1987, Smith et al. 1988, Allison 1990; but see Dahl and Strandhede 1996), whereas the predator satiation hypothesis has been applied to species suffering seed predation by species-specific predators, mainly insects, at the pre-dispersal seed stage (Nilsson and Wästljung 1987; but see Sperens 1997).

Silvertown (1980) stated that synchronous seed production, both between individuals in the same population and between populations of sympatric species sharing the same seed predators, has an advantage of predator satiation. In other words, predator satiation operates on a guild having the same specific predators. Because of the similar morphology and chemical composition of their seeds, congeneric species often have common seed predators. Therefore, interspecific masting among co-occurring congeneric species may have an advantage of predator satiation as masting at the guild level (Shibata et al. 1998).

Manuscript received 20 September 2000; revised 1 June 2001; accepted 4 June 2001; final version received 22 August 2001.

⁶ E-mail: shibarin@ffpri.affrc.go.jp

Evidence for the predator satiation hypothesis is also found in community-level masting, if there are generalist seed predators in a community (Janzen 1974). In several temperate forests that have simple floristic composition, synchronized heavy seed crops among dominant trees cause a population increase of generalist seed consumers such as wood mice (McShea 2000). In tropical forests in Southeast Asia that have high tree diversity, nearly all dipterocarp species heavily flower and fruit together with species of other families in the same year, a phenomenon called general flowering (Ashton et al. 1988, Sakai et al. 1999). Such large fluctuation in the seed production of a community is also reported from seasonal tropical forest in Central America by Wright et al. (1999). The synchronized, episodic reproduction in a community influences movement patterns and local population fluctuations of generalist seed predators and ensures seedling establishment (Wright et al. 1999, Curran and Leighton 2000). Therefore, general flowering is probably a result of a reproductive strategy such as predator satiation (Janzen 1974), although Sakai et al. (1999) emphasized that the general flowering phenomenon might have been adopted because of the efficiency of pollinator attraction.

Ogawa Forest Reserve, an old-growth forest in Japan, has the highest tree diversity of any temperate deciduous forest (Masaki et al. 1999). In this community, we have observed that many species belonging to different taxa have annual fluctuation of seed production synchronized with dominant *Fagus* species, whereas other species produce seeds constantly. However, we have not previously made any formal test of intra- and interspecies synchronized reproduction.

In this forest, more than half of the principal tree species have wind-pollinating systems and pre-dispersal seed predation by insects has been observed for seeds of many species (Tanaka 1995, Shibata et al. 1998; Ueda 2002). Several genera such as *Fagus*, *Quercus*, *Acer*, and *Carpinus* have co-occurring congeneric species. It is possible that these species satiate pre-dispersal seed predators at the population or guild level (Shibata et al. 1998).

In addition, predation by wood mice as generalist seed predators is severe for postdispersal seeds of many species (Tanaka 1995, Iida 1996, Masaki et al. 1998, Ueda 2002). Among the principal tree species, *Fagus* species produce large seeds with high protein and lipid content (Miguchi 1994). If seed consumption by the generalist predators is biased toward nutritious, large acorns in a mast year, and the predators are satiated, other tree species might show increased postdispersal seed survival and seedling emergence. Such predator satiation may operate to facilitate synchronized annual seed production at the community level.

To examine the cause and consequence of synchronized annual fluctuation of seed production in a community, it is valuable to test hypotheses of masting in a population and at the guild and community levels. In

this study, we have four objectives: (1) to examine the masting habit of each species and interspecific synchronization of annual seed production, (2) to test the pollination efficiency hypothesis for the populations of wind-pollinated species, (3) to test the predator satiation hypothesis for the populations and guilds (or groups of congeneric species) that may have specific seed predators such as insects at the pre-dispersal stage, and (4) to test the predator satiation hypothesis for a forest community that may have generalist seed predators such as wood mice at the postdispersal stage.

STUDY SITE AND SPECIES

Ogawa Forest Reserve

This study was conducted in a 6-ha permanent plot in the 100-ha Ogawa Forest Reserve (OFR), located in the southern part of the Abukuma Mountains, Ibaraki Prefecture, central Japan (36°56' N, 140°35' E, elevation 610–660 m). Mean monthly temperature is 9.0°C, with the highest monthly mean of 20.5°C in August and the lowest of –1.6°C in February. Annual precipitation is ~1750 mm. Precipitation is greatest in August and September and least in December and January. Maximum snow depth is about 50 cm.

This forest is an old-growth temperate deciduous forest. There are over 50 woody species (dbh \geq 5 cm) in the 6-ha plot. Detailed descriptions of the structure and dynamics of the community have been made by Masaki et al. (1992, 1999), and Nakashizuka et al. (1992). The Forest Reserve has been protected from human activities for at least 80 yr. Dominant canopy species are *Quercus serrata*, *Fagus japonica*, and *F. crenata*. Plant nomenclature follows Satake et al. (1989).

Sixteen of the principal tree species, including these three dominant species, were chosen for the study (Table 1). Flowering usually occurs in July for *Castanea crenata*, in August for *Kalopanax pictus*, and from early to mid-May for the other 14 species. Seedfall occurs from late October to early December. Seedlings of *C. crenata* emerge from June to July, and the other 15 species emerge from late April to June (Shibata and Nakashizuka 1995).

Seed predators

Insect seed predators at the pre-dispersal stage were investigated for several species in Japanese cool temperate forests, including OFR (Table 2). *Quercus serrata* and *Q. crispula* shared common seed predators, and some of the seed predator species of *Castanea crenata* (*C. sikkimensis*, Blastobasidae sp.) also eat seeds of both *Quercus* species (Ueda 2002). In OFR, most of the seeds of *F. crenata* with internal damage were judged to have been attacked by moth larvae, *Pseudopammene fagivora* Komai species (Ueda 2002). We have not identified seed predators of *F. japonica*, but it is highly probable that the predators were common to the two *Fagus* species: predation marks by the

TABLE 1. List of studied species, with measures of stem density, basal area, and seed mass, along with the pollination system and the number of sample trees and flowering observation years needed to calculate Kendall's coefficient of concordance (W) of flowering within a population.

Species, by family	Code	Density (no./ha)	Basal area (m ² /ha)	Pollination	Seed mass (g)	No. samples to calculate W	No. years to calculate W
Aceraceae							
<i>Acer mono</i>	ACM	29.5	0.89	entomophily	0.023	22	7
<i>Acer amoenum</i>	ACA	81.2	0.92	entomophily	0.008	27	7
Araliaceae							
<i>Kalopanax pictum</i>	KAP	3.0	0.69	entomophily	0.002	17	6
Betulaceae							
<i>Betula grossa</i>	BTG	6.5	0.58	anemophily	0.0005	28	8
<i>Carpinus cordata</i>	CRC	84.8	0.68	anemophily	0.008	27	7
<i>Carpinus japonica</i>	CRJ	11.3	0.28	anemophily	0.005	15	7
<i>Carpinus laxiflora</i>	CRL	88.5	1.36	anemophily	0.003	34	7
<i>Carpinus tschonoskii</i>	CRT	15.8	0.61	anemophily	0.015	11	7
<i>Ostrya japonica</i>	OSJ	12.0	0.83	anemophily	0.006	22	8
Cornaceae							
<i>Swida controversa</i>	SWC	25.0	1.16	entomophily	0.032	61	4
Styracaceae							
<i>Styrax obassia</i>	STO	95.5	0.8	entomophily	0.120	no data	no data
Fagaceae							
<i>Fagus crenata</i>	FGC	18.8	2.77	anemophily	0.109	43	9
<i>Fagus japonica</i>	FGJ	113.8	6.66	anemophily	0.121	35	8
<i>Quercus crispula</i>	QRC	9.5	1.2	anemophily	1.600	30	6
<i>Quercus serrata</i>	QRS	55.3	8.58	anemophily	0.810	72	6
<i>Castanea crenata</i>	CSC	10.8	1.34	entomophily	1.460	no data	no data
Total for studied species		650.5	28.01				
Total for all species in 6-ha plot		864.2	32.35				

Notes: Individual sample trees are more than the minimum reproductive size. Flowering censuses of the sample trees have been continuously done for more than four years.

insects on *F. japonica* were very similar to those on *F. crenata* (M. Shibata, *personal observation*; N. Kamata, *personal communication*). Although the species have not been identified, it is also highly possible that the four *Carpinus* species and *Ostrya japonica* share a common insect seed predator; predation marks by insects on the *Carpinus* species and on *O. japonica* were similar. On the other hand, it appears that species of insect predators differed between the two *Acer* species, based on differences in predation marks made by the insects (Tanaka 1995).

Two wood mouse species, *Apodemus speciosus* and *A. argenteus*, consume seeds at the postdispersal stage of *Fagaceae* species (Sone and Takano 1991, Iida 1996, Ueda 2002), *Acer* spp. (Tanaka 1995), *Carpinus* spp. (M. Shibata, *personal observation*), *O. japonica*, *Styrax obassia* (Sone and Takano 1991), and *Swida controversa* (Masaki et al. 1998) in this forest. Predation by mice is the main mortality factor for these species from autumn (seedfall season) to the next spring (emergent season; Tanaka 1995, Iida 1996, Masaki 1998). For instance, Tanaka (1995) estimates that mice consumed >80% of seeds of *Acer* species in winter.

METHODS IN FIELD AND LABORATORY

Individual flowering synchrony

We investigated the flowering synchrony within a population (from 18 to 191 individual trees) for each

species in the 6-ha plot. We observed the individual trees with binoculars and checked whether they flowered or not in every flowering season from 1987 to 1995. Kendall's coefficient of concordance (W) was used to assess the degree of synchrony of flowering within a population. To calculate W of flowering, we selected sample trees that were larger than the minimum reproductive tree size and for which flowering censuses had been continuous for at least four years (Table 1). The smallest sample size of observations was 11 individuals of *Carpinus tschonoskii* and the largest was 72 individuals of *Quercus serrata*. We did not calculate W of flowering for *Styrax obassia* and *Castanea crenata* because we did not have data on the individual flowering of these species.

Production of male flowers, seeds, and seedlings in a population

We measured seed production of the 16 species from 1987 to 1995 and staminate aments (male flowers) of five *Fagaceae* and six *Betulaceae* species from 1988 to 1995. In the center of the 6-ha plot at OFR, a 1.2-ha subplot has been established for intensive investigations of seed and seedling demography since autumn in 1987 (Shibata and Nakashizuka 1995, Tanaka and Nakashizuka 2002). Densities of reproductive trees of each species in the 1.2-ha subplot were comparable to those of the 6-ha plot. For the present study, we ana-

TABLE 2. List of pre-dispersal insect seed predators on study species in Ogawa Forest Reserve (OFR) and elsewhere in Japan.

Tree species code†	Predators			Research site	Reference
	Type	Order	Species		
ACM, ACA	fly larvae moth larvae, lace bugs	Diptera Lepidoptera Tingidae	<i>Xynottingis hoytona</i>	OFR	Tanaka (1995)
KAP	no predation marks de- tected			OFR	
BTG	no predation marks de- tected			OFR	
CRC, CRJ, CRL, CRT	weevil larvae	Curculionidae	<i>Curculio</i> spp.	OFR	Shibata et al. (1998)
OSJ	unknown, but similar to <i>Carpinus</i> spp.			OFR	
SWC STO	unknown weevil larvae	Curculionidae	<i>Curculio styra- cis</i>	OFR	S. Abe, <i>per- sonal com- munication</i>
FGC	moth larvae	Tortricidae	<i>Pseudopam- mene fagivo- ra</i>	northern part of main is- land of Ja- pan, OFR	Igarashi and Kamata (1997), Ueda (2002)
	moth larvae	Geometridae	<i>Venusia phas- ma</i>		
FGJ	moth larvae unknown, but similar to FGC	Argyresthiidae		OFR	
QRC, QRS	weevil larvae	Curculionidae	<i>Curculio sikki- mensis</i>	Hokkaido	Maeto (1995)
	weevil larvae	Curculionidae	<i>Curculio disti- guendus</i>	OFR	Ueda (2002)
	weevil larvae	Curculionidae	<i>Curculio denti- pes</i>		
	moth larvae	Tortricidae	<i>Cydia danilev- skyi</i>		
	moth larvae	Tortricidae	<i>Cydia glandi- colana</i>		
	moth larvae	Blastobasidae			
CSC	weevil larvae moth larvae	Curculionidae Blastobasidae	<i>Curculio sikki- mensis</i>	OFR	Ueda (2002)

† See Table 1 for species codes.

lyzed data from 121 seed traps that were placed in a regular grid (10 × 10 m) in the 1.2-ha subplot, and had been set continuously during the whole study period from 1987 to 1995. The seed traps had a surface area of 0.5 m² and were made of nylon cloth (mesh size 1 mm). They were set ~1.0 m above the ground. During the study period, we collected contents of the seed traps and brought them back to the laboratory every four weeks from April to August and every two weeks from September to December.

In the laboratory, we sorted the staminate aments of 11 species belonging to Fagaceae and Betulaceae from the contents of the seed traps and weighed them after oven-drying (80°C, 3 d). We used the dry mass (in

grams per square meter) of staminate aments as an index of the quantity of pollen. We counted all seeds of the 16 species and cut them open to classify them into five categories: (1) sound (attaining mature seed size with a sound cotyledon and/or endosperm); (2) immature (failing to attain mature seed size); (3) empty (attaining mature seed size but with the embryo undeveloped or lacking); (4) holed (having a gnawing mark or hole caused by insect predation); and (5) broken (mainly caused by vertebrate predation). Detailed descriptions of these methods are also available in Shibata et al. (1998). Average density (number per square meter) of the seeds of each category falling into a seed trap was calculated every year. Dry mass of kernels of

sound seeds (including cotyledon, hypocotyl, radicle, and endosperm, if present, but excluding seed coat and any dispersal structure) was measured to estimate a seed mass for each species (Tanaka et al. 1998).

A 1-m² seedling quadrat was set adjacent to every seed trap. We investigated seedling emergence from 1988 to 1996. Seedlings that emerged from the quadrats were marked and counted every year. Detailed descriptions of this investigation are available in Shibata and Nakashizuka (1995) and Tanaka and Nakashizuka (2002). Average density (number per square meter) of seedlings emerging in a quadrat was calculated every year. The percentage of seedling emergence was estimated as the ratio of the average density of seedlings emerging the next year to the average density of sound seeds.

ANALYSES

Fluctuation and synchronization of annual seed production

To examine the intensity of the masting habit of each species, we correlated the CV of the number of sound seeds as an index of annual fluctuation of seed production in a population. We used Kendall's coefficient of concordance (W) of flowering condition (flowering vs. nonflowering) as an index of the synchrony of flowering among individuals in a population. These two variables were also correlated after controlling for phylogenetic effects using the independent-contrasts method, CAIC (Purvis and Rambaut 1995). The phylogeny of species in this study was based on Chase et al. (1993).

To examine the interspecific synchronization of annual seed production, we first calculated Kendall's rank correlation matrix of the annual sound seed production among species. Then we applied cluster analysis (by the group average method) to the matrix data. Dissimilarity was obtained by transforming the correlation coefficients of Kendall's rank correlation (τ , with values ranging from -1 to 1) into dissimilarity coefficients (D , ranging from 0 to 1) by the equation:

$$D = (-\tau + 1)/2.$$

Cause and consequences of intra- and interspecific synchronization of annual seed production

Smith et al. (1990) state that two important conditions are necessary if masting is to confer an advantage for efficient pollination: (1) the cost of sexual reproduction through female function must be the same regardless of fertilization success, and (2) fluctuations in male and female reproductive efforts must be positively correlated across years (synchronous).

For the 11 species whose staminate ament production could be estimated, we tested the pollination efficiency hypothesis. Ten of these are wind-pollinated species and one (*Castanea crenata*) is insect pollinated. We

examined whether or not these species satisfied the two conditions, and whether their pollination efficiency increased as pollen increased. Specifically, we investigated the abortion behavior of each species by field observation and literature searches. We calculated time series cross-correlations with zero-year lag between the quantity of staminate aments and the number of total seeds (the sum of the number of seeds in all categories [sound, empty, immature, holed, and broken]) and the percentage of mature seeds (the ratio of the number of sound, holed, and broken seeds to total seeds, i.e., the percentage of fertilized seeds).

To assess whether the annual fluctuation of seed production is related to predator satiation, three elements are needed: (1) the production of enough seeds to satiate predators, ensuring that some seeds escape; (2) the production of few seeds to starve predators before the next large production year; and (3) synchronous seed production, both between individuals in the same population and between populations of sympatric species having the same seed predators (Silvertown 1980). The 14 species for which we detected insect predation marks were used to test the predator satiation hypothesis at the pre-dispersal seed stage. The sum of the number of sound and holed seeds was used for an index of the potential seed production to insects' food. The number of sound and holed seeds (log-transformed) was correlated with the percentage of insect predation (the ratio of the number of holed seeds to that of sound plus holed seeds) to examine the satiation of insect predators.

We tested three groups for the number of sound and holed seeds: Prsa1, seeds of the same species; Prsa2, seeds of congeneric species; and Prsa3, seeds of species that are assumed to have common seed predators. Group Prsa1 was used to test for predator satiation at the population level, whereas groups Prsa2 and Prsa3 were used to test for predator satiation in a guild that has common predators.

To examine the starvation of predators by annual fluctuation of seed production, the ratio of the total number of sound and holed seeds in the current year to that in the previous year can be a useful index (Mattson 1978, Shibata et al. 1998). If seed predation depends on the density (population size) of predators, which is controlled by the insects' food in the previous year, a negative correlation can be expected between this ratio and the percentage of insect predation (Mattson 1978). The potential predator-starving effect of fluctuating annual seed production was tested for the 14 tree species using these variables. We tested three types of ratios: Prst1, seeds of the same species; Prst2, seeds of congeneric species; and Prst3, seeds of species that are assumed to have common seed predators. These analyses were time series cross-correlations with one-year and two-year lags.

To test the satiation of generalist predators at the postdispersal stage (from seed fall season to seedling

emergence season), the quantity of sound seeds (the number of sound seeds multiplied by the average mass of a sound seed kernel) was correlated with the percentage of seedling emergence the next year. We adopted not the number, but the quantity, of the seeds as an independent variable, because (1) generalist seed predators at the post-dispersal stage such as wood mice eat various sizes of seeds (Table 1), and (2) the value (impact) of each seed as a predator's food roughly depends on its size.

We tested three types of quantities of sound seeds: Posa1, seeds of all the principal tree species (the 16 species, representing almost all of the vegetable food source for wood mice in a whole community); Posa2, seeds of the two *Fagus* species (nutritious acorns favored by wood mice in this forest); and Posa3, seeds of the five Fagaceae species (all acorns that account for a large part of the wood mouse food supply). This analysis was a time series cross-correlation with one-year lag, and was applied to nine species that usually do not form a seed bank. Four out of the nine species have relatively small seeds (mass 0.003–0.023 g) and the others have large seeds (mass 0.1–1.6 g).

We expected that the percentage of seedling emergence would be positively correlated with the sum of the quantity of seeds of all the principal tree species (type Posa1) for the nine species if predator satiation were to operate in a whole community. If seed consumption by the generalist predators is biased toward nutritious and/or large acorns in a mast year, and the predators are satiated, less nutritious and/or smaller seeds (i.e., those less attractive to mice) will be expected to survive more successfully and to have a high percentage of seedling emergence. Therefore, we expected to find that not only the percentage of seedling emergence of the two *Fagus* species, but also that of other species, would be positively correlated with the seeds of the two *Fagus* species (type Posa2), if less nutritious seeds could avoid predation through predator satiation by large crops of nutritious acorns in a community. The percentage of seedling emergence would be positively correlated with the seeds of the five Fagaceae species (type Posa3), not only for the five Fagaceae species but also for the others, if small seeds could avoid predation because of predator satiation by large crops of acorns in a community.

When a variable of a species was correlated with a single variable of the species, we evaluated statistical significance at the $P = 0.05$ level for each species test. When the same variable was correlated with multiple variables, we calculated a lower critical P value using the Bonferroni procedure. For example, significance levels of $P = 0.05$, 0.01 , and 0.001 were corrected to $P = 0.05/9$, $0.01/9$, and $0.001/9$ when the quantity of the seeds was correlated with the percentage of seedling emergence of each of the nine species in the test of the generalist predator satiation. SYSTAT (SYSTAT 1992) was used to calculate Kendall's coefficient of concor-

dance (W) of flowering and for the cluster analysis; JMP (SAS Institute 1995) was used for all other statistical analyses.

RESULTS

Fluctuation and synchronization of annual seed production

We found that many tree species in the Ogawa Forest Reserve showed highly fluctuating annual production of sound seeds (Fig. 1). They produced more seeds in particular years (1988, 1990, 1993, and 1995), although a few species like *Quercus serrata* and *Q. crispula* kept producing a relatively constant number of seeds.

Among the tree species, values of Kendall's coefficient of concordance (W) of flowering ranged from 0.01 to 0.49 and values of the cv of annual production of sound seeds ranged from 0.61 to 2.69. Four *Carpinus* spp., two *Fagus* spp., and *Kalopanax pictus* showed the strongest masting habits of all species analyzed (Fig. 2). They had a higher W of flowering within a population and a higher cv of annual sound seed production. In contrast, both of these values were lowest for the two *Quercus* species, indicating that their masting habits were the weakest of all species studied. These two indices of masting habit, i.e., W of flowering and the cv of annual sound seed production, varied continuously among species, suggesting no clear boundary between masting and nonmasting habits (Fig. 2).

There was a positive correlation between W of flowering and the cv of annual sound seed production ($r = 0.720$, $P < 0.01$). This positive relationship, however, was not significant after controlling for phylogenetic effects using the independent-contrasts method ($r = 0.038$). Species belonging to the same genus had similar values of the two indices, except for the genus *Fagus*. On the other hand, there was large difference among species belonging to the same family, e.g., Fagaceae.

Kendall's rank correlation analysis of patterns in annual production of sound seed showed that 11 of the 16 species had a significant positive correlation with at least three of the other species. This indicates that tree species in this forest had multiple species synchronizing their annual production of sound seed (Appendix A). *Quercus serrata* and *Q. crispula* had a significant positive correlation with each other, but not with the other species. *Betula grossa*, *Fagus crenata*, and *Castanea crenata* did not have a significant positive correlation with any of the other species, showing rather independent patterns.

Cluster analysis of the 16 species based on dissimilarity of the rank correlation coefficient showed two major clusters (Fig. 3). We classified one major cluster into three small clusters. The largest one included 11 species (*K. pictus*, *Ostrya japonica*, four *Carpinus* species, *Styrax obassia*, *Swida controversa*, two *Acer* spe-

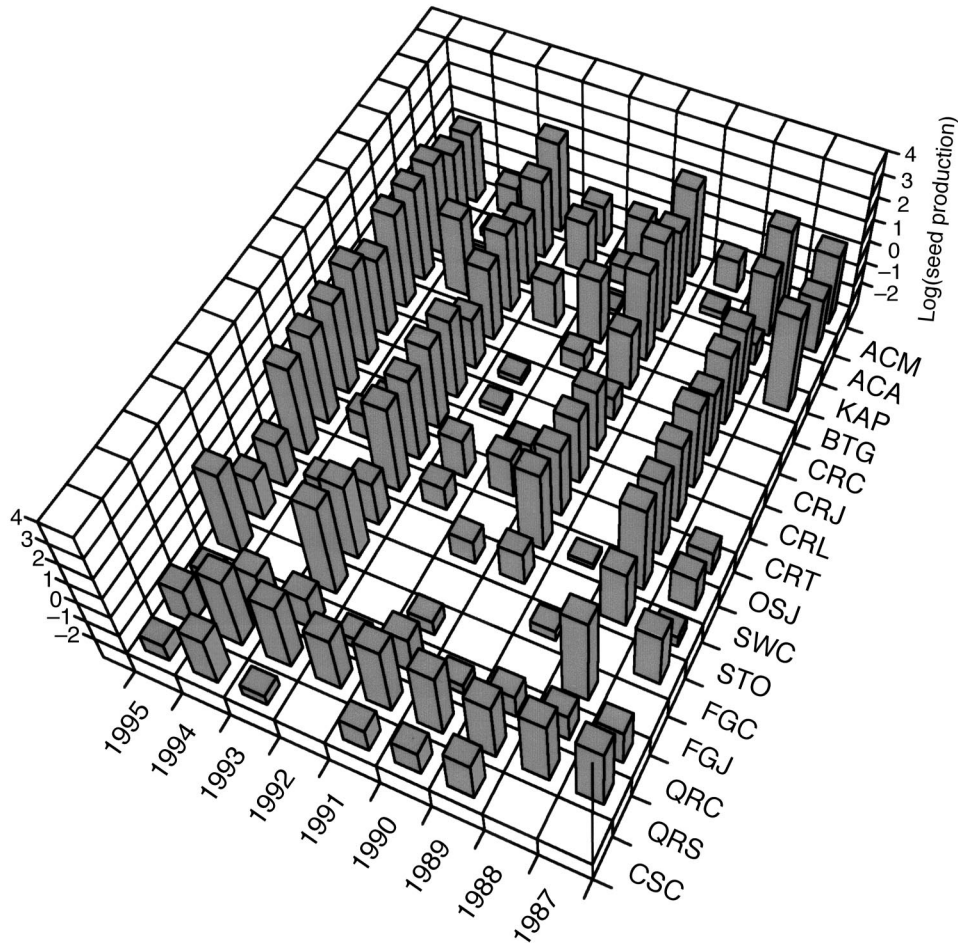


FIG. 1. Annual fluctuation of sound seed production (number per square meter, log-transformed) of the principal tree species in Ogawa Forest Reserve, Japan. Codes for the species names here and in all other figures are shown in Table 1.

cies, and *Fagus japonica*). The others included one species each (*Betula grossa* and *F. crenata*). The second major cluster was classified into two small clusters, one including two *Quercus* species and the other consisting only of *C. crenata*. All congeneric species were included in the same major cluster. Dissimilarity was small among all of the congeneric species, especially in the genus *Carpinus*.

Pollination efficiency

The number of total seeds (the sum of the number of seeds belonging to all categories) was significantly proportional to the quantity of staminate aments for five species (Fig. 4; Appendix B). The other species (except *B. grossa*) also had a positive coefficient of correlation (ns, $P > 0.05$). The ovaries or seeds of the species of Betulaceae and the two *Fagus* species mostly grow to normal, mature size, and many of their fruiting branches and acorns do not shed, regardless of successful fertilization (Shibata et al. 1998; Appendix B). In contrast, unfertilized ovaries of two *Quercus* species and *C. crenata* fall at an early stage of seed develop-

ment and do not grow to mature size (Matsuda 1982, Sork 1993). Thus, the two necessary conditions for a pollination advantage from masting, stated by Smith et al. (1990), were satisfied for five species of Betulaceae and Fagaceae (*Carpinus cordata*, *C. laxiflora*, *C. tschonoskii*, *O. japonica*, and *F. japonica*) in this forest.

Carpinus cordata, *C. laxiflora*, and *C. tschonoskii* showed a significant positive correlation between the quantity of staminate aments (pollen) and the percentage of mature seeds (Fig. 4; Appendix B). *Ostrya japonica* had a marginally significant positive correlation, and *C. japonica*, *Q. crispula*, and *Q. serrata* had a weak positive correlation, partly explained by the short observation period. In contrast, *F. crenata*, *F. japonica*, *C. crenata*, and *B. grossa* did not have such a positive relationship.

Pre-dispersal seed predation

A negative correlation between the percentage of insect predation and the sum of the number of sound and holed seeds was significant for *C. cordata*, *C. japonica*, *C. laxiflora*, *O. japonica*, *S. controversa*, *F.*

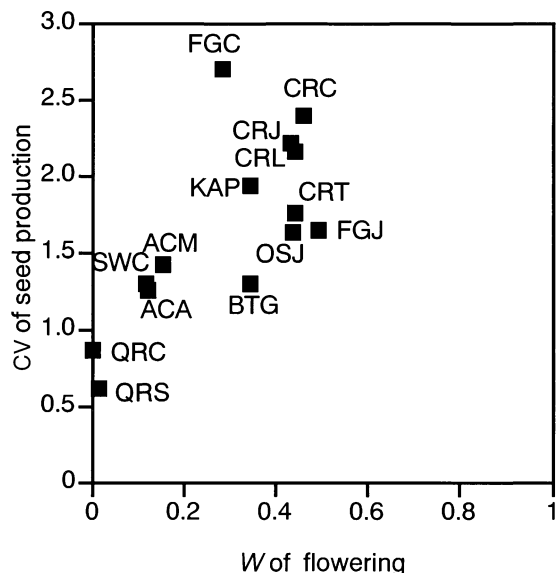


FIG. 2. Relationship between the coefficient of variation (cv) of annual sound seed production and Kendall's coefficient of concordance (W) of flowering individuals in each population.

japonica, and *Q. serrata* (Fig. 5; Appendix C). *Acer amoenum*, *C. tschonoskii*, and *F. crenata* had a marginally significant correlation with high correlation coefficients, partly because of the short observation period. This tendency was also observed when the seeds were pooled among the congeneric species or among the species that may have common seed predators (Fig. 5; Appendix C). *Carpinus tschonoskii* and *Q. crispula*, which showed relatively low correlation coefficients when they were analyzed as a single species, showed larger correlation coefficients when the seeds of the

species were pooled with those of congeneric species and/or species that may have common predators. However, for *C. crenata*, which has some of the same seed predators as the two *Quercus* species, the negative correlation was weaker when the seeds were pooled.

There was a negative correlation between the percentage of insect predation and the ratio of the number of sound and holed seeds in year N to that in year $N - 1$ for *C. cordata*, *C. japonica*, *C. laxiflora*, *S. controversa*, *F. japonica*, and *C. crenata* (Fig. 6; Appendix D). *Acer amoenum* had a marginally significant correlation. The other seven species had a weak negative correlation (NS, $P > 0.05$). A negative correlation was also observed when the seeds of congeneric species, and of species that may share common seed predators, were pooled (Fig. 6; Appendix D). For *C. laxiflora* and *Q. serrata*, we found a significant negative correlation between the two factors when seeds of the species were pooled among congeneric species.

A negative correlation between the percentage of insect predation and the ratio of the number of sound and holed seeds in year N to that in year $N - 2$ was significant for *Q. crispula* and *Q. serrata* (Fig. 6; Appendix E), strongly suggesting that the populations of seed predators of these two *Quercus* species were controlled by the seed production of two years before. In contrast, the other species did not show a negative relationship between these variables. We also found a significant negative correlation when the seeds of these two *Quercus* species were pooled. However, for *C. crenata*, we found no such relationship.

Postdispersal seed predation

Acorn production of five species of *Fagaceae* constituted a large part (50–99.9%) of the sound seed production by all the 16 species. This is probably the most

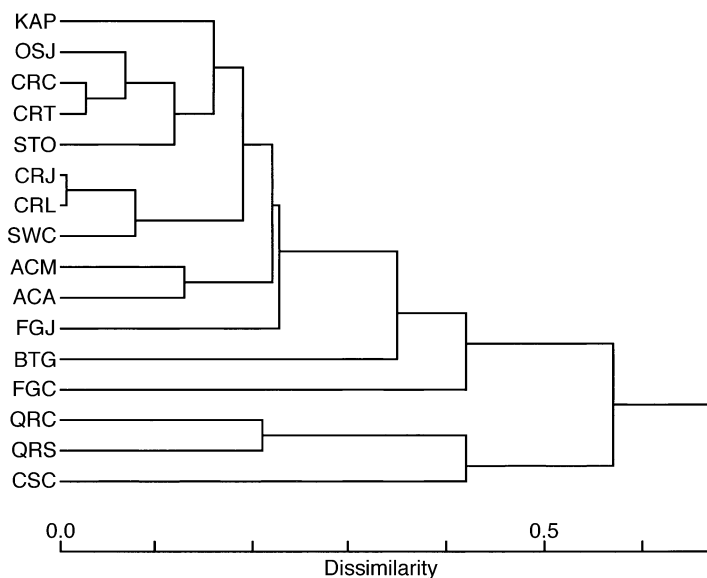


FIG. 3. Dendrogram obtained by cluster analysis of annual seed production of 16 principal tree species in the Ogawa Forest Reserve. See Table 1 for species codes.

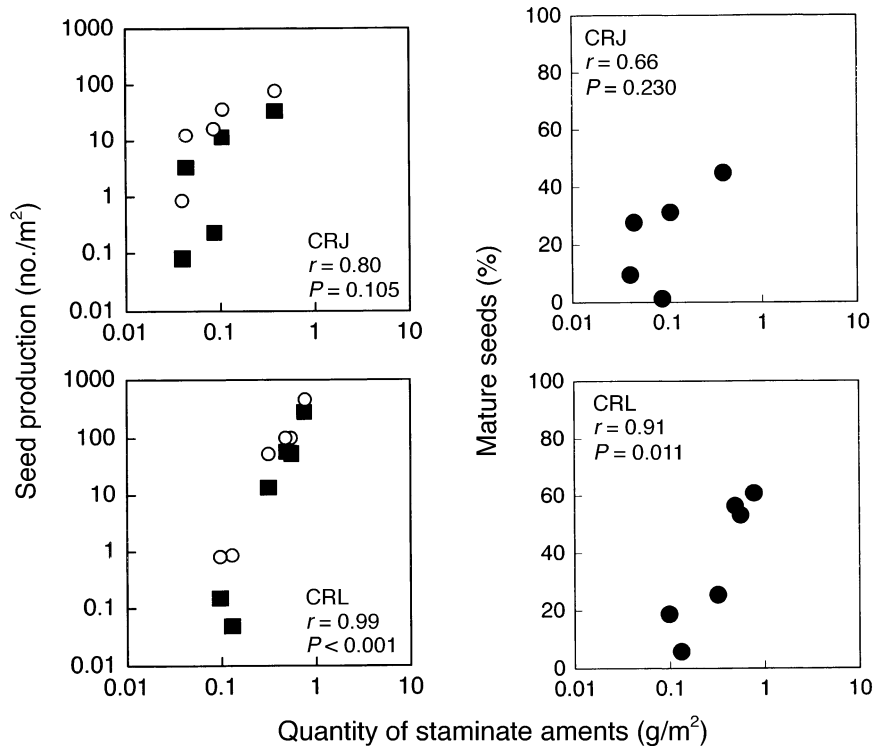


FIG. 4. Evaluation of pollination efficiency: the relationships between the quantity of staminate aments and the number of seeds produced (left), and the percentage of mature seeds (right). Open circles indicate total seed number, including sound, holed, broken, immature, and empty seeds. Solid squares indicate mature seed number, including sound, holed, and broken seeds. Note the double log scales.

valuable food resource for wood mice during winter in this forest community (Fig. 7). In addition, seed production of *F. japonica*, with its nutritious acorns, was the main contributor to the large annual fluctuation of food resources for wood mice in this forest.

None of the types of sound seed production tested was clearly correlated with the percentage of seedling emergence, although a possible reason for this lack of relationship was the small number of observation years (Appendix F). When the percentage of seedling emergence was correlated with the quantity of seeds of all the principal species, and with the quantity of seeds of five Fagaceae species, *C. japonica*, *F. crenata*, and *F. japonica* had a relatively large positive correlation coefficient (NS, $P > 0.05$), but the other species had a low or negative one. When the percentage of seedling emergence was correlated with the quantity of seeds of two *Fagus* species, *C. japonica*, *F. crenata*, *F. japonica*, and *C. crenata* had a relatively large positive correlation coefficient (NS, $P > 0.05$), but the other species tended to have a low or negative one.

These results suggest that only one of the four species with small seeds had the potential to escape from predation via predator satiation by the seed production of other species, especially those with large and/or nutritious seeds. *Fagus crenata* and *F. japonica* showed positive (but not significant) relationships between the

percentage of seedling emergence and all types of sound seed production. This suggests that postdispersal predator satiation may have operated on populations of *Fagus* species, but not on the whole community.

DISCUSSION

Masting habit of each species and interspecific synchronization of annual seed production

There are two essential conditions for the masting habit: large annual fluctuations in seed production and the synchronization of that fluctuation among individuals (Kelly 1994). Many studies have discussed the annual fluctuation of seed production at the population level, but only a few studies have quantitatively recorded and discussed the synchronization of flowering (or seeding) among individuals (Herrera 1998). Results of our quantitative analysis of both conditions (Fig. 2) showed that the extent of annual fluctuation and synchronization were positively correlated in this forest community. In addition, the extent of the masting habit varied continuously among species, as Kelly (1994) and Herrera et al. (1998) observed. Thus, it was difficult to find a marked boundary between masting and nonmasting species.

Masting has been recorded and discussed mainly for a single or a few dominant tree species (populations)

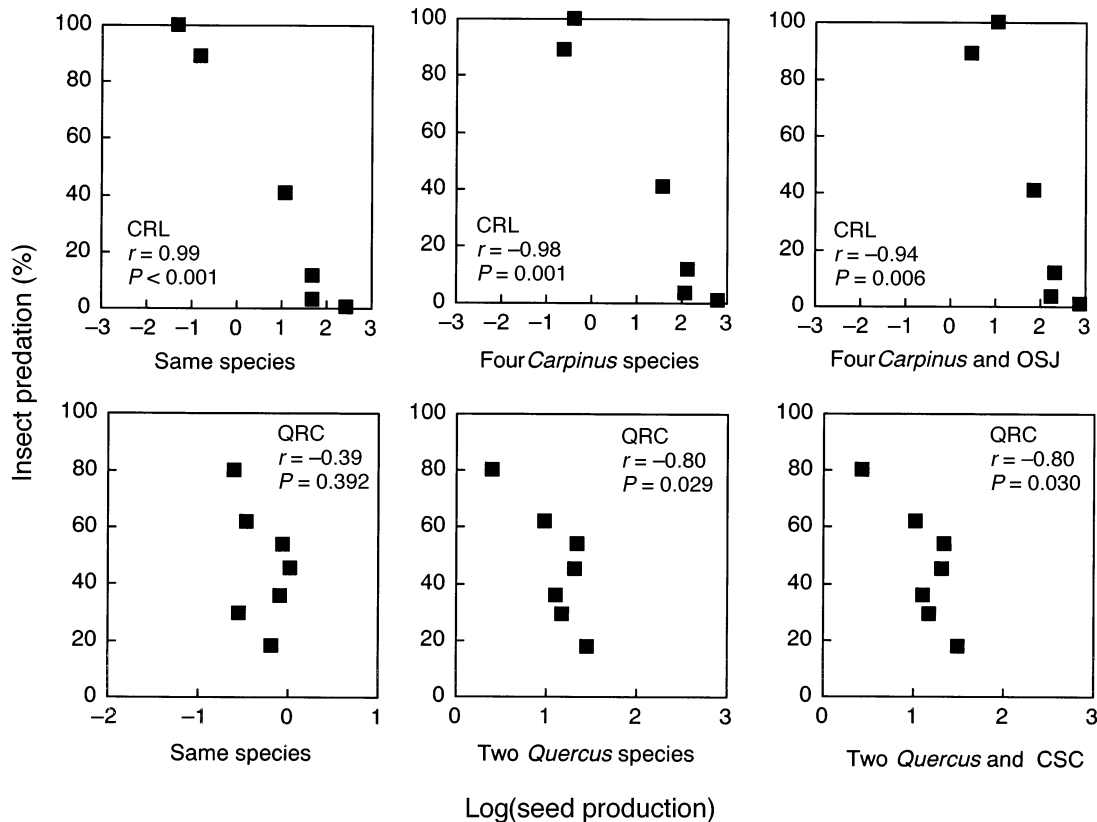


FIG. 5. Evaluation of predator satiation at the pre-dispersal seed stage. The sum of the number of sound and holed seeds is used as an index of the potential seed production (number of seeds per square meter) for insects' food. The relationship between the percentage of insect predation and the log-transformed sum of the number of sound and holed seeds is shown. We tested three groups for the number of sound and holed seeds: seeds of the same species (left); seeds of congeneric species (center); and seeds of species that are assumed to have common seed predators (right).

in a community. Synchronous gregarious flowering in a tropical rain forest in Southeast Asia has been the rare case for which the synchronous flowering was discussed as a community-level phenomenon (Sakai et al. 1999). A comparison of the patterns of annual seed production among the 16 principal tree species in the Ogawa Forest Reserve community showed that synchronized annual seed production occurred among congeneric species (Figs. 1 and 3; Appendix A). In addition, the positive relationship between the extent of the masting habit (Fig. 2) did not hold after controlling for phylogenetic effects. These results suggest that the annual flowering habit of trees is firstly phylogenetically constrained. Because closely related species may have similar physiological requirements and response thresholds of flowering to environmental factors, it would be expected that flowering and fruiting patterns of taxonomically related species are more similar to each other (i.e., synchronous) than are the patterns shown by species that are more taxonomically distant. However, we should be careful to note that phylogenetic relations also affect, indirectly, the interaction with seed predators through regulation of morphological traits. We also found that even taxonomically dis-

tant species showed synchronized annual seed production with each other (Figs. 1 and 3; Appendix A), whereas some species in the same family did not synchronize (e.g., families Fagaceae and Betulaceae). There was a large variation in the degree of masting habit even within a family (Fig. 2). Both physiological regulation and adaptive significance should be considered to explain the diverse patterns of the annual fluctuation of flowering (seeding) in a community.

Other life history traits such as phenology of flowering, flower sex expression, and pollination system may also be related to the patterns of annual seed production. *Castanea crenata*, alone, represented a unique group of seed production among the analyzed species. This species has a unique phenology, flowering late in mid-June, whereas the other species flower in early to mid-May, and is the only one entomophilous species of Fagaceae in this forest. Different environmental and phenological conditions for pollination and seed development of this species are reflected in the different pattern of annual seed production. *Acer rufrinerve*, which has a unique sex-changing habit, also showed quite different annual flowering and seeding pattern from the other *Acer* species studied (Tanaka 1995).

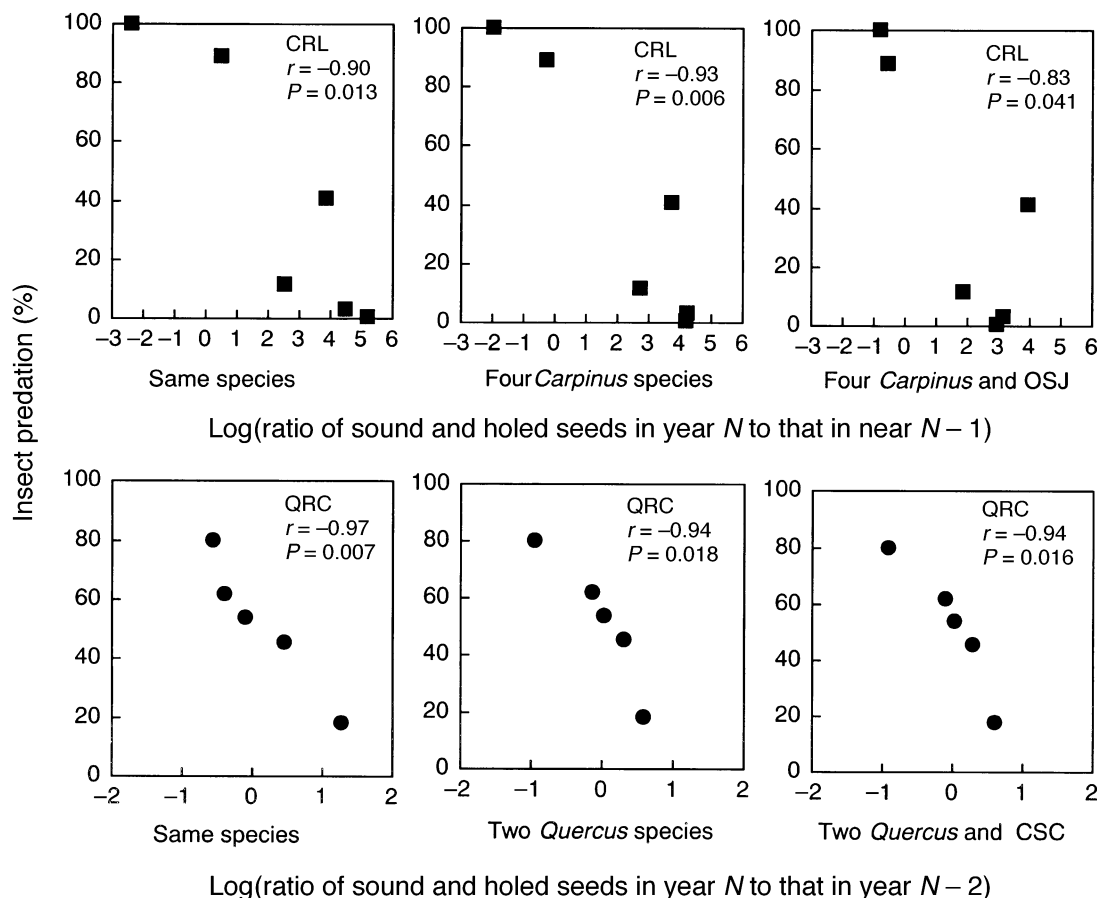


FIG. 6. Evaluation of predator starvation at the pre-dispersal seed stage: relationship between the percentage of insect predation and the log-transformed ratio of the sum of the number of sound and holed seeds in year N to that in year $N - 1$ (or $N - 2$). We tested three groups for the number of sound and holed seeds, as in Fig. 5.

It has also been claimed that disturbance-dependent species tend not to have the mast-seeding habit (Barnes et al. 1998). Mast-seeding species must lose their chances for regeneration when unpredictable disturbances occur during the nonmast years, if they do not form a seedling bank on the forest floor. Among wind-pollinated species, including the two *Quercus* species in this forest, the size distribution index (SDI) of a population (Hubbell 1979, Masaki et al. 1992, 1999) was negatively correlated with the cv of sound seed production ($r = 0.773$, $P < 0.01$). This result means that species with large SDI (having small saplings and juveniles on the forest floor, and thus requiring episodic events such as large disturbance for regeneration) have weak masting habits.

Pollination efficiency in a population

The pollination efficiency hypothesis was fully supported by our results for the reproductive traits of three species, *C. laxiflora*, *C. tschonoskii*, and *C. cordata* (Appendix B). This hypothesis probably would be supported for *O. japonica* and *C. japonica* if we were to loosen the conditions or get more long-term data for

this analysis. However, *B. grossa* and two *Fagus* species, which did not have a positive correlation between the quantity of staminate aments and the percentage of mature seeds, contradicted this hypothesis. Two *Quercus* species that showed relatively constant annual seed production, as well as *C. crenata*, satisfied neither of the two necessary conditions, having shed most of their ovaries at an early stage of seed maturation. The shedding of ovaries (or seeds) could occur as a result of fertilization failure and/or abortion due to resource deficiencies in reproductive organs. Sork (1993) also suggested that the annual fluctuation of seed production of *Quercus* species in a North American temperate forest was more affected by seed survival during the process from pollination to maturation than by the quantity of flowering staminate aments. Annual fluctuation of seeds may be better explained by resource matching for these *Quercus* species.

Recently, resource budget models for masting that consider pollen limitations have been proposed (Isagi et al. 1997, Satake and Iwasa 2001). The models were constructed based on the resource-matching hypothesis, and could represent various patterns of synchro-

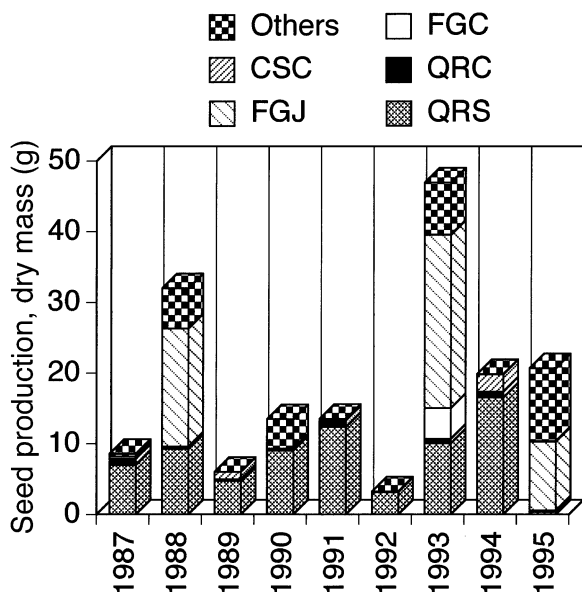


FIG. 7. Annual fluctuation in the quantity of seed production in Ogawa Forest Reserve, Japan, shown as the sum of the dry mass of sound seed kernels. Seed quantity of each Fagaceae species is shown independently, whereas the values of the other 11 species are combined and shown together. See Table 1 for species codes.

nized annual fluctuation of seed production by using two parameters, i.e., cost of reproduction and outcrossing pollen limitation. To further understand the relative importance of pollination efficiency for the masting habit, it is necessary to estimate the resource allocation to the reproductive organs and verify this resource budget model.

All wind-pollinated species that were found to have the advantages of pollination efficiency were classified into the same small cluster (Fig. 3). This indicates that highly synchronized annual seed production (and/or flowering) occurred among the species. In the case of animal-pollinated species in a lowland dipterocarp forest in Malaysia, the advantage of synchronized flowering among species could be that the aggregated flowering of various species having common pollinators may activate these pollinators and result in higher pollination success than with isolated flowering (Sakai et al. 1999). However, for wind-pollinated species, there are no such advantages for interspecific synchronized flowering. Pollination efficiency should work as an effective selection pressure among individuals in a wind-pollinated population independently.

Satiation of species-specific predators at the pre-dispersal seed stage

Pre-dispersal seed predator satiation at the population level was statistically significant in six out of 14 species: *C. cordata*, *C. japonica*, *C. laxiflora*, *S. controversa*, *F. japonica*, and *Q. serrata* (Appendices C–E). They satiate predators in large seed crop years, and

reduce the populations of predators in poor seed years to obtain high seed survival in the following good seed years. Although the other species did not show significant correlations, every species had negative correlation coefficients (Appendices C, D, and/or E). We think that satiation and starvation of species-specific predators at the pre-dispersal seed stage might operate for these species, and will be detected when we get more long-term data.

The starving effect during poor seed years usually appeared in one-year intervals. However, the interval depends on the length of the life cycle of the seed-eating insects. Several insects have life cycles that last more than one year because of very slow growth, repeated or prolonged dormancies, or very long-lived adults (Danks 1992). Menu and Debouzie (1993) found that chestnut weevil (*Curculio elephas*) larvae, which were predators of *Castanea sativa* in France, had a plastic trait of dormancy and usually took one or two years to grow into adults. K. Maeto (*personal communication*) found that weevil larvae of *Q. crispula* took two years to grow into adults. He also found a significant negative correlation between the percentage of acorns suffering predation and the ratio of seed production in year N to $N - 2$ in a north-temperate oak (*Q. crispula*) forest in Hokkaido, Japan. The two *Quercus* species in the Ogawa Forest Reserve also showed a negative relationship between the percentage of insect predation and the ratio of the number of sound and holed seeds in year N to that in year $N - 2$ (Fig. 6; Appendix E), suggesting that their main seed predators had a life cycle of two years. In contrast, the main seed predators of *Carpinus*, *Fagus*, *Castanea*, and *Swida* should have a life cycle of one year in this forest, because their host trees showed a significant negative correlation between these variables with one-year lag, but not between those with a two-year lag (Appendix E).

Satiation of guild-specific predators at the pre-dispersal seed stage

Specific relationships between a guild of seed producers and insect predators will facilitate the synchronization of fluctuating seed production between different tree species. In this forest, synchronous seed production was observed not only among individuals in the same population, but also among populations of the same or related genera (Figs. 1 and 3). In addition, similar predation marks were found on the seeds of different species that all showed synchronized seed production. These findings strongly suggest the existence of common seed predators (except for two *Acer* species), although the insect predators have not been completely identified for each tree species.

We also found evidence of satiation and starvation of pre-dispersal seed predators for the species groups that synchronize seed production, i.e., in genera *Quercus*, *Fagus*, *Carpinus*, and *Ostrya* (Appendices C–E). These co-occurring congeneric species could obtain

mutual benefits by synchronizing their seed production to satiate their common insect seed predators. However, two species of Fagaceae (*Q. serrata* and *Q. crispula*), which have common seed predators, showed evidence of predator satiation and starvation, but neither had a strict masting behavior (Fig. 2). Therefore, the benefits may not always work solely as a selection pressure for large annual fluctuation of seed production (masting).

*Satiation of generalist predators at the
postdispersal seed stage*

Satiation of wood mice at the postdispersal seed stage has been observed in monodominant beech and oak forests (Boucher 1981, Miguchi and Maruyama 1984). However, in this species-rich deciduous forest, there were no clear relationships between seed production and seedling emergence (Appendix F). Therefore, we did not detect the ecological advantage of postdispersal generalist predator satiation at the community level that Janzen (1974) suggested.

One of the reasons for the failure of predator satiation at the community level may be loose synchronization of annual seed production in Fagaceae species, all of which have large acorns. It is possible that stable seed production of *Q. serrata* and independent annual seed production of *C. crenata* may guarantee the food resources for wood mice (Fig. 7). Hoshizaki and Hulme (2001) investigated seed survival of *Aesculus turbinata* (a nonmasting species with seed including saponins) in a forest dominated by beech (*F. crenata*, a masting species without defensive chemicals) where wood mice were the major generalist seed predators. Although seed survival of *A. turbinata* in autumn was high in the mast years of beech, its survival rate until the next spring (germination season) was lower than that in the nonmast years of beech. Hoshizaki and Hulme (2001) suggested that mast seed production of beech kept the mouse population high in the winter season and indirectly caused the high mortality of *A. turbinata* in early spring after *Fagus* seeds germinated. Such differences in annual seeding habits, quality or palatability as food, and seedfall and germinating phenology, may also complicate the actual operation of predator satiation at the postdispersal seed stage.

*Proximal cue of synchronized reproduction
among species*

It is interesting that many species with different pollination systems or predators have synchronized annual fluctuation of reproduction in a temperate forest community (Fig. 3). Several studies have proposed that weather is linked to the mechanisms of synchronized annual flowering and seed fluctuation of each population. Because weather factors that are sensed by all individuals in a population and occur only once every several years would be limited, the flowering trigger of each species would tend to be common (Sakai et al. 1999). A proximal cue of synchronized flowering in a

dipterocarp forest may be an increase in sunshine or drought (Wood 1956, Cockburn 1975, Van Schaik 1986; but see Sakai et al. 1997, Yasuda et al. 1999). However, recent studies have linked a drop in daily minimum temperature caused by El Niño–Southern Oscillation (Ashton et al. 1988) or by La Niña (Yasuda et al. 1999) to the general flowering. It is also reported that high or low temperature has triggered flower bud initiation in temperate forests (Forcella 1981, Norton and Kelly 1988, Allen and Platt 1990). To clarify the relationship among weather factors, reproductive phenology, and ecological significance at the community level, we should collect longer time series data of annual seed production in a community, coupled with some physiological experiments.

CONCLUSION

We demonstrated that there was continuous variation in the strength of masting habit and that many species belonging to different taxa had annual fluctuation in seed production synchronized with one of the dominant species (*Fagus japonica*) in this species-rich forest community. Even conducting the study for more than a decade might not be long enough to reveal the strong-masting species with long intermast interval (e.g., *F. crenata*) and related phenomena, our nine-year study could observe at least two good seed years for those tree species. The data obtained from this long-term observation enabled us to test hypotheses related to masting at various levels from population to community. In addition, results of this study were consistent with those of former analyses using seven years of data for *Carpinus* (Shibata et al. 1998), suggesting the robustness of the present analyses.

Although our results have some insufficiency of statistical significance, they show that predator satiation, both at the population and guild level, effectively operated for many species, providing the advantage of better seed survival at the pre-dispersal stage. Pollination efficiency was likely to be operating at the population level for half of the wind-pollinated species. For some species, resource matching appears to be the most important mechanism for variable seed production. However, generalist predator satiation at the post-dispersal seed stage may not operate in a simple, detectable manner in this community.

At present, we cannot totally explain the mechanisms and adaptive significance of the interspecific synchrony of reproduction. However, it is highly probable that the combined effects of several factors (e.g., limited weather triggers for flowering, common flowering physiology among taxonomically related species, and ecological advantages at the population and guild levels), may cause multiple species to have synchronized fluctuation patterns of seed production. Individuals of the same and closely related species may have similar physiological requirements for flowering (or fruiting) and they may respond to the same meteorological conditions for

flowering. The ecological advantages of pollination efficiency at the population level, and pre-dispersal seed predator satiation at the population and guild levels, could work as selection pressure to stabilize synchronized annual fluctuation of reproduction.

ACKNOWLEDGMENTS

We would like to thank S. J. Wright for his helpful advice and critical reading of the manuscript; K. Maeto, A. Ueda, N. Kamata, and H. Fukumoto for their help in the laboratory and many discussions; and M. Suginuma and I. Fushimi for their help with the laboratory work. Kind and detailed suggestions were received from M. Abrams and three anonymous reviewers. This research was supported, in part, by a grant from the Ministry of Agriculture, Forestry and Fisheries (Bio-Cosmos Project), Ministry of Education, Science and Culture (09NP1501), and the Environment Agency (Global Environment Research Fund, B-52-(3)-2).

LITERATURE CITED

- Allen, R. B., and K. H. Platt. 1990. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* **57**:199–206.
- Allison, T. D. 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. *Ecology* **71**:516–522.
- Ashton, P. S., T. J. Givnish, and S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the seasonal tropics. *American Naturalist* **132**:44–66.
- Barnes, V. B., D. R. Zak, S. R. Denton, and S. H. Spurr. 1998. Regeneration ecology in forest ecology. Fourth edition. John and Wiley, Philadelphia, Pennsylvania, USA.
- Boucher, D. H. 1981. Seed predation by mammals and forest dominance by *Quercus oleoides*, a tropical lowland oak. *Oecologia* **49**:409–414.
- Chase, M. W., et al. 1993. Phylogenetics of seed plants: an analysis of nucleotide sequence from the plastid gene *rbcl*. *Annals of the Missouri Botanical Garden* **80**:528–580.
- Cockburn, P. S. 1975. Phenology of dipterocarp in Sabah. *Malaysian Forester* **44**:28–36.
- Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Bornean Dipterocarpaceae. *Ecological Monographs* **70**:101–128.
- Dahl, A., and S. Strandhede. 1996. Predicting the intensity of the birch pollen season. *Aerobiologia* **12**:97–106.
- Danks, H. V. 1992. Long life cycles in insects. *Canadian Entomologist* **124**:167–187.
- Forcella, F. 1981. Ovulate cone production in pinyon: negative exponential relationship with late summer temperature. *Ecology* **62**:488–491.
- Herrera, C. M. 1998. Long-term dynamics of mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* **68**:511–538.
- Herrera, C. M., P. Jordano, J. Guitián, and A. Traveset. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist* **152**:576–594.
- Hoshizaki, K., and P. E. Hulme. 2001. Mast seeding and predator-mediated indirect interactions in a forest community: evidence from post-dispersal fate of rodent-generated caches. Pages 227–239 in D. J. Levey, W. R. Silva, and M. Galetti, editors. *Seed dispersal and frugivory: ecology, evolution and conservation*. CABI Publishing, Wallingford, Oxfordshire, UK.
- Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**:1299–1309.
- Igarashi, Y., and N. Kamata. 1997. Insect predation and seasonal seedfall of the Japanese beech, *Fagus crenata* Blume, in northern Japan. *Journal of Applied Entomology* **121**:65–69.
- Iida, S. 1996. Quantitative analysis of acorn translocation by rodents using magnetic locator. *Vegetatio* **124**:39–43.
- Isagi, K., K. Sugimura, A. Sumida, and H. Ito. 1997. How does masting happen and synchronize? *Journal of Theoretical Biology* **187**:231–239.
- Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**:69–103.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* **9**:465–470.
- Maeto, K. 1995. Relationship between size and mortality of *Quercus mongolica* var. *grosseserrata* acorns due to pre-dispersal infestation by frugivorous insects. *Journal of the Japanese Forestry Society* **77**(3):213–219.
- Masaki, T., W. Suzuki, K. Niiyama, S. Iida, H. Tanaka, and T. Nakashizuka. 1992. Community structure of a species-rich temperate forest, Ogawa Forest Reserve, central Japan. *Vegetatio* **98**:97–111.
- Masaki, T., H. Tanaka, M. Shibata, and T. Nakashizuka. 1998. The seed bank dynamics of *Cornus controversa* and their role in regeneration. *Seed Science Research* **8**:53–63.
- Masaki, T., H. Tanaka, H. Tanouchi, T. Sakai, and T. Nakashizuka. 1999. Structure, dynamics and disturbance regime of temperate broad-leaved forests in Japan. *Journal of Vegetation Science* **10**:805–814.
- Matsuda, K. 1982. Studies on the early phase of the regeneration of a konara oak (*Quercus serrata* Thunb.) secondary forest. I. Development and premature abscissions of konara oak acorns. *Japanese Journal of Ecology* **32**:293–302.
- Mattson, W. J. 1978. The role of insects in the dynamics of cone production of red pine. *Oecologia* **33**:327–349.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* **81**:228–238.
- Menu, F., and D. Debouzie. 1993. Coin-flipping plasticity and prolonged diapause in insects: example of the chestnut weevil *Curculio elephas* (Coleoptera: Curculionidae). *Oecologia* **93**:367–373.
- Miguchi, H. 1994. Role of wood mice on the regeneration of cool temperate forest. Pages 115–121 in *Proceedings of NAFRO seminar of sustainable forestry and its biological environment*. Northeast Asia Forest Research Organization, Niigata, Japan.
- Miguchi, H., and K. Maruyama. 1984. Ecological studies on a natural beech forest (XXXVI). Development and dynamics of beechnuts in a mast year. [In Japanese with English summary.] **66**:320–327.
- Nakashizuka, T., S. Iida, H. Tanaka, M. Shibata, S. Abe, T. Masaki, and K. Niiyama. 1992. Community dynamics of Ogawa Forest Reserve, a species-rich deciduous forest, central Japan. *Vegetatio* **103**:105–112.
- Nilsson, S. G., and U. Wästljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* **68**:260–265.
- Norton, D. A., and D. Kelly. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* **2**:399–408.
- Purvis, A., and A. Rambaut. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analyzing comparative data. *Computer Applications in the Biosciences* **11**:247–251.
- Sakai, S., K. Momose, T. Inoue, and A. A. Hamid. 1997. Climate data in Lambir hills National Park and Miri Airport, Sarawak. Pages 1–10 in T. Inoue and A. A. Hamid, editors. *Canopy biology program in Sarawak II: general*

- flowering of tropical rain forests in Sarawak, 1–10. Center for Ecological Research, Kyoto University, Otsu, Japan.
- Sakai, S., K. Momose, T. Yumoto, T. Nagamitsu, H. Nagamasu, A. A. Hamid, T. Nakashizuka, and T. Inoue. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* **86**: 1414–1436.
- SAS Institute. 1995. JMP user's guide. Version 3.1 of JMP. SAS Institute, Cary, North Carolina, USA.
- Satake, Y., H. Hara, S. Watari, and T. Tominari, editors. 1989. Wild flowers of Japan, Woody plants, I, II. [In Japanese.] Heibonsha, Tokyo, Japan.
- Satake, A., and Y. Iwasa. 2001. Pollen-coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology* **203**(2):63–84.
- Shibata, M., and T. Nakashizuka. 1995. Seed and seedling demography of four co-occurring *Carpinus* species in a temperate deciduous forest. *Ecology* **76**:1099–1108.
- Shibata, M., H. Tanaka, and T. Nakashizuka. 1998. Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. *Ecology* **79**:54–64.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* **14**:235–250.
- Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1988. The effects of stand density on frequency of filled seeds and fecundity in lodgepole pine (*Pinus contorta* Dougl.). *Canadian Journal of Forest Research* **18**:453–460.
- Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1990. The advantage of mast years for wind pollination. *American Naturalist* **136**:154–166.
- Sone, K., and H. Takano. 1991. Applicability of artificial burrows to studies of natural populations of two species of wood mice, *Apodemus speciosus* and *A. argenteus*. *Journal of the Japanese Forest Society* **73**(3):238–241.
- Sork, V. L. 1993. Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *Vegetatio* **107/108**:133–147.
- Sperens, U. 1997. Fruit production in *Sorbus aucuparia* L. (Rosaceae) and pre-dispersal seed predation by the apple fruit moth (*Argyresthia conjugella* Zell.). *Oecologia* **110**: 368–373.
- SYSTAT. 1992. SYSTAT: Statistics. Version 5.2 edition. SYSTAT, Evanston, Illinois, USA.
- Tanaka, H. 1995. Seed demography of three co-occurring Acer species in a Japanese temperate deciduous forest. *Journal of Vegetation Science* **6**:887–896.
- Tanaka, H., and T. Nakashizuka. 2002. Ground design of the research site. Pages 43–49 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and interaction in a temperate forest community. Springer-Verlag, Tokyo, Japan.
- Tanaka, H., M. Shibata, and T. Nakashizuka. 1998. A mechanistic approach for evaluating the role of wind dispersal in tree population dynamics. *Journal of Sustainable Forestry* **6**(1/2):155–174.
- Ueda, A. 2002. Interactions between seeds of family Fagaceae and their seed predators. Pages 285–298 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and interaction in a temperate forest community. Springer-Verlag, Tokyo, Japan.
- Van Schaik, C. P. 1986. Phenological change in a Sumatran rain forest. *Journal of Tropical Ecology* **2**:327–347.
- Wood, G. H. S. 1956. Dipterocarp flowering season in Borneo. *Malaysian Forester* **19**:193–201.
- Wright, S. J., C. Carrasco, O. Caloeron, and S. Paton. 1999. The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* **80**:1632–1647.
- Yasuda, M., J. Matsumoto, N. Osada, S. Ichikawa, N. Kachi, M. Maki, T. Okuda, A. Fukuhara, A. R. Nik, and N. Manokaran. 1999. The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology* **15**:437–449.

APPENDIX A

A table presenting a rank correlation (Kendall's tau) matrix of annual sound seed production of 16 tree species in Ogawa Forest Reserve, Japan, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-026-A1.

APPENDIX B

A table showing pollination efficiency (quantity of staminate aments, total seeds, and percentage of mature seeds) for 14 tree species in Ogawa Forest Reserve, Japan, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-026-A2.

APPENDIX C

A table evaluating predator satiation at the pre-dispersal stage for seeds of 14 tree species in Ogawa Forest Reserve, Japan, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-026-A3.

APPENDIX D

A table evaluating predator starvation at the pre-dispersal stage for seeds of 14 tree species in Ogawa Forest Reserve, Japan, with correlations for years N to $N - 1$, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-026-A4.

APPENDIX E

A table evaluating predator starvation at the pre-dispersal stage for seeds of 14 tree species in Ogawa Forest Reserve, Japan, with correlations for years N to $N - 2$, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-026-A5.

APPENDIX F

A table evaluating predator satiation at the postdispersal stage for seeds of nine tree species in Ogawa Forest Reserve, with correlations of the quantity of sound seeds and percentage of seedling emergence, is available in ESA's Electronic Data Archive: *Ecological Archives* E083-026-A6.