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A Five-Year Study of Mast Seeding in *Pinus densiflora*

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I examined the annual pattern of seed production in three Korean populations of *Pinus densiflora* from 1998 to 2002. During the fall season, data were collected on the numbers of cones per tagged tree, as well as seed counts, their mass, and seed set following dehiscence. Dbh was measured for individual trees during each spring. Overall, 80.3% of the trees produced seed cones in even-numbered years compared with 51.6% in odd-numbered years. Moreover, trees that matured seed cones in even years produced 12 times more seeds per tree than those in odd years. Tree diameters generally increased significantly during the summers after odd-numbered years, although the trees at one site showed a consistent growth rate each year after 2000. Annual variations in individual seed mass, seed set, and the proportion of damaged seed cones occurred largely within odd or even years. Based on these results, the following conclusions were made: 1) seed-cone production of *P. densiflora* is somewhat synchronized, but is not an all-or-nothing phenomenon, 2) *P. densiflora* tends to undergo mast seeding at two-year intervals, and 3) this alternate-year excess in seed crop may have evolved to increase fitness, though the exact evolutionary mechanism is unclear.

Keywords: dbh growth, *Pinus densiflora*, seed crop, seed predation, seed set

Many trees as well as herbs undergo mast seeding in tropical to boreal areas (Kelly and Sork, 2002). That is, these plants produce a large seed crop in good years but little or none in poor years, thereby affecting the feeding activity of seed predators and, consequently, seed or seedling mortality. Several hypotheses have been proposed to account for this pattern of seed production (Sork, 1993; Kelly, 1994; reviewed in Kelly and Sork, 2002). The most parsimonious explanation is resource-matching, although this implies only a proximate mechanism. According to this hypothesis, plants produce massive seed crops once in a few years, only when resources are abundant. Therefore, good crops are associated with optimal weather conditions in the current and/or immediately preceding years (Lester, 1967; Sharp and Sprague, 1967; Caron and Powell, 1989; Sork and Bramble, 1993; Mäkinen, 1998). However, researchers have found no such correlation when tested with species that occur over large geographic areas (Koenig and Knops, 2000).

On the other hand, the bimodal patterns of mast seeding over an extended period of time (Norton and Kelly, 1988) and the differential inter-masting periods of related species that coexist in the same habitat (Sork and Bramble, 1993) suggest that mast seeding may not occur simply to match levels of resources that change with temperature or rainfall. That is, mast seeding may be an evolved phenomenon. In fact, a trade-off relationship between tree-ring growth and mast seed crop has been proposed as strong evidence of selection for mast seeding because it indicates resource-switching from vegetative to reproductive growth (Tappeiner, 1969; Koenig and Knops, 1998; Houle, 1999).

Most recent studies have attempted to evaluate the relative importance of selection for efficient pollination and predator satiation. With the pollination efficiency hypothesis, mast seeding is explained as an indirect outcome of selection for efficient pollination or outcrossing (Norton and Kelly, 1988; Smith et al., 1990). For wind-pollinated species, male fitness increases disproportionately over a range of male efforts (Lloyd, 1984; Schoen et al., 1986). Critical evidence for this hypothesis is the increase in pollination and seed set following mast flowering, as has been reported in *Taxus canadensis* (Allison, 1990), *Picea mariana* (Caron and Powell, 1989), four *Carpinus* species (Shibata et al., 1998), *Fagus sylvatica* (Nilsson and Wästljung, 1987), and *Picea abies* (Mencuccini et al., 1995). Fitness-gain from mast flowering may be greater for plants that invest a large amount of resources in flowers before fertilization and for those that produce concordant numbers of male and female flowers across years (Smith et al., 1990). That assumption is particularly pertinent to gymnosperms as most of them expend a great deal of energy in female flowers

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following pollination, but before fertilization.

Seed predators including vertebrates and insects eat a large portion of pine seeds, acorns, or beechnuts before and after seed dispersal (Smith, 1970; Bossema, 1979; Marchelli and Gallo, 1999). The predator satiation hypothesis states that mast seeding may have evolved by selection to avoid seed loss by satiating seed predators (Janzen, 1971; Silvertown, 1980) or to attract generalist dispersers (Bawa, 1980). The best evidence for this is the increased probability of seed survival from predation during mast years (Sork, 1993). For example, in beech, predation by moth larvae in mast years is only about one-tenth of that in non-mast years (Nilsson and Wästljung, 1987).

In this study, seeding patterns were evaluated from *Pinus densiflora* in mixed stands with oak, two species that codominate the forests of Korea. Previous studies on seeding or seed predators of *P. densiflora* were conducted only for a single or, at most, a couple of years (e.g., Hong and Rim, 1997; Kang, 1999; Park, 2002). However, a relatively long time period is required if one is to identify cyclic patterns. Furthermore, the synchronicity among *P. densiflora* trees within populations has not been quantitatively examined, not to mention the mechanisms for mast seeding. Here, the relationship between dbh growth and size of seed crop was also tested over several years to confirm that mast seeding is an evolved phenomenon. The following questions were examined: 1) to what extent do the trees within populations synchronize seed production; 2) what is the pattern of seed crops over five years; 3) is there a trade-off relationship between dbh growth and seed crop; and 4) do seed set and seed predation rates change across years?

MATERIALS AND METHODS

Study Sites

In Spring 1998, *P. densiflora* trees were randomly tagged at three sites: 1) Mt. Kwanak (KA, N = 35) (37° 26′N, 126° 58′E); 2) Hongneung (HN, N = 31) (37° 35′N, 127° 03′E); and 3) Yeoju (YJ, N = 41) (37° 17′N, 127° 45′E). The first two populations in Seoul, were 17 km apart, while the third, in Kyunggi-do, was about 70 km from both KA and HN. In 1999, two trees were added to each site, although the other two died at KA in 2002. All of these sites were mixed forests of *P. densiflora*, *P. rigida*, *Robinia pseudoacacia*, and various *Quercus* species.

Data Sets

Using binoculars, I counted the number of matured seed cones on each tagged tree just before they dehisced each fall, from mid- to late September, 1998 to 2002. Up to ten cones were then collected from different sides of each tree, and were kept in envelopes at room temperature until their seeds were released about two months later. Afterward, I noted the condition of the cones as being dehisced, undehisced, damaged by seed predators, or having stunted growth. Seed numbers and their mass per cone were also recorded. Full seeds within a cone were counted and weighed after being separated by gentle pressing from the aborted seeds. Stunted cones, which comprised only 0.9% of those sampled, showed no evidence of filled seeds. Because I assumed that seed numbers did not differ among dehisced, undehisced, and damaged cones, the total seed number per tree was obtained by multiplying the mean seed number per cone by the number of cones on a given tree. Mean individual seed mass for each tree was obtained by dividing total mass by total seed number. The seed set was calculated as the ratio of full seed number to potential seed number (i.e., the number of fertile scales multiplied by two) in each cone. Means of these ratios were multiplied by 100 to estimate seed set per tree. The number of fertile scales of cones was counted only for a portion of the trees in 1998 (11, 5, and 5 trees at KA, YJ, and HN, respectively), but was later tallied for all trees from which cones were sampled. The dbh of each tree was measured at the time of tagging in the spring, from 1998 until 2001 (YJ and HN) or 2002 (KA).

Data Analyses

The pattern of synchrony in seed cone production across sites at each year was examined with two-way categorical analyses (presence vs. absence of seed cones x site). Then the pattern of synchrony across the years and sites was simultaneously tested using log-linear analyses of three categorical variables of seed cone presence vs. absence x year x site. To account for correlations among years within trees, only trees observed for five consecutive years were included in these data. In this analysis, only two sites, KA and YJ, were considered because Site HN contained one empty cell, i.e., absence of trees without seed cones in 2000. The association between year and seed cone condition was evaluated using a two-way contingency table analysis on data pooled over all sites because expected cell counts of damaged and stunted seed cones were low in most combination cells of year x seed cone condition.

Although the same trees were observed over five years, data were incomplete. For example, two trees died during the study period, and some measurements, such as cone crops, could not be obtained for some trees with dense canopies, especially at YJ and HN, in at least one year. Thus, for variables such as cone crops, seed number per cone, and total crops per tree, the results for annual patterns of variation were first presented using data pooled over all trees at each site. Afterward, the results of the repeated-measures ANOVAs were provided, using the data from trees with complete information over five consecutive years. In 2002, seed cones at HN were sampled only from four trees due to their heights. Thus, repeated-measures ANOVAs for total seed crops per tree were applied twice using five-year data, including all three sites as well as those excluding HN. Repeated-measures ANOVAs on dbh were conducted using four-year data (for all three sites) or five-year data (for KA only). The significance of each contrast in repeated-measures ANOVAs was tested after a Bonferroni correction to maintain an overall alpha of 0.05 (von Ende, 2001). Seed mass and seed set could not be analyzed by repeated-measures ANOVAs because many trees lacked data due to low cone production in poor years. Thus, the potential factors affecting seed mass and seed set were examined using a nested ANOVA with year, site, and trees within sites as the three main factors. Subsequently, differences in yearly patterns for those seed variables were evaluated separately for each site with a two-way ANOVA, with year and tree identity as main factors.

All dependent variables, except individual seed mass, were log-transformed to improve the normality of the data. Means were provided with 1 SD throughout this study. All analyses were conducted with version 8.1 of SAS (1999).

RESULTS

Synchrony of Seed Cone Production across Years

The overall proportion of *P. densiflora* trees that bore seed cones varied greatly from year to year, but their annual patterns were quite consistent among the three sites. When averaged over all populations, 80.4% (1998), 46.9% (1999), 88.2% (2000), 56.0% (2001), and 72.1% (2002) of trees produced seed cones (Table 1). Overall, 1.6 times higher proportions of trees produced seed cones-80.3% versus 51.6%-in even-numbered years (1998, 2000 and 2002) than in odd-numbered years (1999 and 2001). However, not all trees bore seed cones even in those better years, except at HN in 2002, while at least 25.6% of those trees produced seed cones in poor years, e.g., YJ in 1999. The proportion of trees producing cones differed among the three sites in all years except for 2001 (Table 1). This was largely because those at YJ were always less likely to have good cone crops regardless of the year; in fact, even in the "good" year of 2002, only 48.8% of the YJ trees produced cones. However, when simultaneously tested, seed cone presence vs. absence was significantly associated with both year and site, but without a significant year x site interaction (Table 2). A reduced model without the interaction term confirmed the results of the saturated model (Table 2). All parameters representing the intervals of years were significant at alpha < 0.01. Based on these results, I concluded that 1) *P. densiflora* tended to produce seed cones at two-year intervals,

Table 1. Frequency distribution of *P. densiflora* trees bearing seed cones for five years (1998 to 2002). Presence and absence refer to trees bearing ≥ 1 seed cones and those bearing no cones, respectively.

Year		Kwanak	Yeoju	Hongneung	X^2	P
1998	Presence	32	25	29	15.90	0.0004
	Absence	3	16	2		
1999	Presence	21	11	21	13.00	0.0015
	Absence	16	32	12		
2000	Presence	35	29	33	15.32	0.0005
	Absence	2	11	0		
2001	Presence	21	19	21	2.03	0.3629
	Absence	15	21	12		
2002	Presence	27	21	32	22.14	< 0.0001
	Absence	8	22	1		

Table 2. Log-linear analyses of site x year x seed cone presence vs. absence. Only trees of *P. densiflora* at two sites [KA (N = 33) and YJ (N = 36)], which were consistently observed over five years, were included in analyses.

Source	df	G	P	Total N
A. Saturated model				69
Intercept	1	103.34	<0.0001	
Site	1	12.44	0.0004	
Year	4	46.51	<0.0001	
Site x Year	4	2.54	0.6375	
Residual	0	.	.	
B. Reduced model				69
Intercept	1	112.50	<0.0001	
Site	1	19.94	<0.0001	
Year	4	46.01	<0.0001	
Residual	4	2.54	0.6375	

2) the synchrony of cone production among trees within sites was not an all-or-nothing phenomenon, and 3) the degree of synchrony differed among sites.

Annual Pattern of Seed Cone Crops

The crop of seed cones per tree fluctuated by 12.4-fold over five years, with the annual pattern being similar to the synchronicity of cone production. Overall, it was higher in even-numbered years, i.e., 1998, 2000 and 2002, than in 1999 and 2001 (Fig. 1A). Thus, ignoring tree identity and site, *P. densiflora* trees produced an average of 11.7 ± 5.6 (N = 328) and 1.9 ± 3.5 (N = 222) seed cones per tree in even and odd years, respectively. However, those three even-numbered years were not identical in terms of their per-tree level of cone crops. For example, that mean averaged over the three sites increased 2.4-fold in 2002 compared with crops in 2001, but was only 21.6% of the crop measured in 1998. The three sites also differed in their five-year cone production (Fig. 1A). In particular, trees at YJ bore on average only one-fifth as many cones as at KA and HN (X = 10.7 ± 5.7, 2.2 ± 4.1, and 10.6 ± 5.3, N = 180, 207, and 163 at KA, YJ, and HN, respectively). However, it should be noted that YJ produced relatively high and low seed-cone crops in 2001 and 2002, respectively, compared with the other sites.

When I included only trees with at least one seed cone, cone crops per tree varied 12.9 times at KA (X = 22.0 ± 3.6, range = 6.1-78.5, N = 136), 4.9 times at YJ (X = 9.2 ± 3.2, range = 4.4-21.5, N = 105), and 11.7 times at HN (X = 18.0 ± 4.0, range = 5.0-58.7, N = 136) across the five years. Therefore, the trees with matured seed cones in even years produced 3.3 times more cones than those in odd years (X = 22.8 ± 3.7 vs. 7.0 ± 2.7 seed cones, N = 263 vs. 114). These results indicated that even vs. odd years differed not only in terms of the proportion of trees producing seed cones but also in the number of matured cones on each tree.

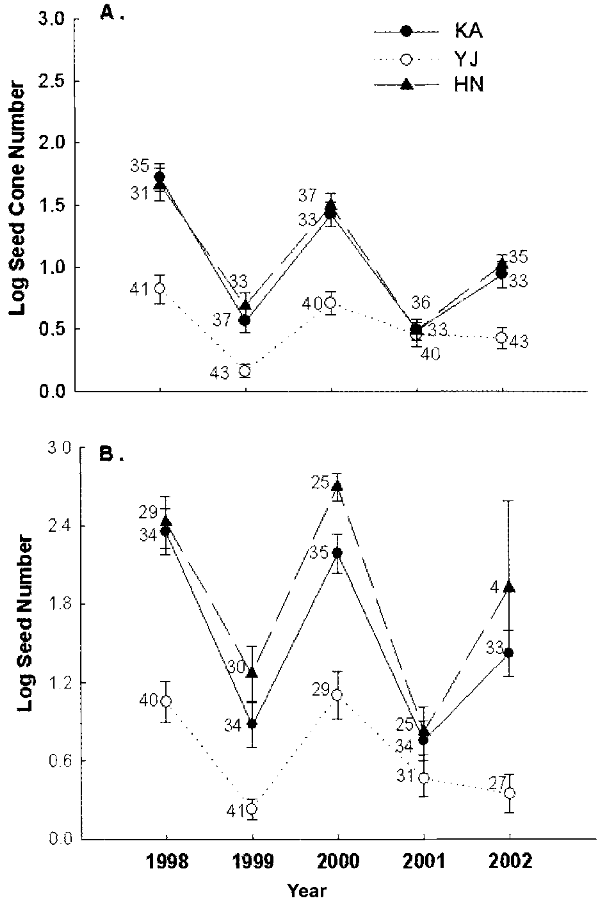

Figure 1. Log of seed cone number per tree (**A**) and log of total seed number per tree (**B**) of *P. densiflora* trees observed for five years at three sites. Numbers next to symbols represent sample sizes.

In repeated-measures ANOVA, the effect of site x year interaction was significant (Table 3). Despite these interaction effects, seed-cone crops per tree, averaged over sites, differed among years (Table 3). Subsequent ANOVAs for each contrast of year showed that cone crops decreased significantly in 1999 and 2001 compared with 1998 and 2000, respectively (Table 4). The change in crops due to site was significant for contrasts 2001-2000 and 2002-2001 (Table 4). Therefore, these results confirmed a different annual pattern of seed-cone crops at YJ from at other sites from 2000 onward (Fig. 1A). Thus, cone crops of *P. densiflora* trees peaked in even years at KA and HN, but those trends were less obvious among trees at YJ.

Table 3. Repeated measures ANOVAs on seed cone numbers, total seed numbers, and dbh of *P. densiflora* trees. Analysis for dbh was conducted using four-year data from KA and YJ, while analyses for other characters were based on five-year data from all three sites. In univariate tests for within-subject effects, probability levels were not adjusted because all Greenhouse-Geisser epsilon values were very high, e.g., ≥ 0.6723.

Source	Seed cones			Total seeds			Dbh		
	df	F	P	df	F	P	df	F	P
Between-subject									
Site	2	16.86	<0.0001	2	6.10	0.0050	1	13.34	0.0004
Error	97			38			106		
Within-subject									
Year	4	87.81	<0.0001	4	13.67	<0.0001	3	9.59	<0.0001
Year x Site	8	5.67	<0.0001	8	1.91	0.0626	3	0.52	0.6687
Error (Year)	388			152			318		

Table 4. ANOVAs for each of the contrasts of within-subject factor (year) for seed cone numbers, total seed numbers, and dbh of *P. densiflora* trees. Analyses were conducted for four-year data (including only two sites for dbh) and for five-year data (including all three sites for the other characters).

Source	Seed cones			Total seeds			Dbh		
	df	F	P	df	F	P	df	F	P
Contrast variable: 1999-1998									
Mean	1	163.2	<0.0001	1	19.71	<0.0001	1	4.31	0.0403
Site	2	2.92	0.0587	2	1.52	0.2324	1	0.15	0.7025
Error	97			38			106		
Contrast variable: 2000-1999									
Mean	1	132.60	<0.0001	1	34.44	<0.0001	1	0.34	0.5585
Site	2	2.45	0.0914	2	2.89	0.0677	1	0.06	0.8135
Error	97			38			106		
Contrast variable: 2001-2000									
Mean	1	165.26	<0.0001	1	38.87	<0.0001	1	45.14	<0.0001
Site	2	18.91	<0.0001	2	7.19	0.0023	1	6.65	0.0113
Error	97			38			106		
Contrast variable: 2002-2001									
Mean	1	37.06	<0.0001	1	5.86	0.0203			
Site	2	10.35	<0.0001	2	2.02	0.1465			
Error	97			38					

Annual Pattern of Total Seed Crops

Total seed production per tree varied widely by site over the five years: 50.5 times (KA), 16.7 times (YJ), and 87.2 times (HN) (Fig. 1B). Most of this variation occurred between even years and odd years (Fig. 1B). Thus, *P. densiflora* trees produced 12 times as much seed in even-numbered years (X = 48.4 ± 15.4 vs. 4.0 ± 8.4, N = 256 vs. 195). When I considered only trees with at least one cone, an average of 185.1 ± 5.8 seeds were produced in even years and 36.7 ± 5.5 seeds in odd years (N = 191 vs. 87). Trees at KA and HN produced more seeds than those at YJ across years (KA X = 33.4 ± 14.4, N = 170; YJ X = 4.4 ± 7.7, N = 168; HN X = 64.2 ± 16.6, N = 113).

A repeated-measures ANOVA showed that the two-way interaction effect on total seed crops was marginally insignificant (Table 3). The change in total seed crops among years due to site was significant only between 2000 and 2001 (Table 4), reflecting that total seed crops per tree at KA and HN in 2001 were only 2.6% and 2.7% of those in 2000, in contrast to 28.5% at YJ during this interval. However, the average for all sites differed significantly among years, indicating that total seed crops were lower in odd years. Considering only KA and HN, only the year effect was significant (site $F_{1,26} = 0.00$, $P = 0.9929$; year $F_{4,104} = 11.68$, $P < 0.0001$; year x site $F_{4,104} = 0.15$, $P = 0.9614$). Total seed crops per tree changed significantly at every interval of years, both for data sets that included all three sites as well as those that contained only KA and HN, although contrast 2002-2001 became insignificant after a Bonferroni correction (Table 4).

The number of seeds within cones varied 1.4 times, 1.7 times, and 2.3 times, respectively, at KA, YJ, and HN over five years. All three factors in a nested ANOVA-year, site, and tree identity within sites-had significant effects on the number of seeds per cone (model $F_{99, 169} = 8.50$, $P < 0.0001$, total $N = 269$; year $F_{4, 169} = 4.29$, $P = 0.0025$; tree identity within sites $F_{93, 169} = 7.16$, $P < 0.0001$; site $F_{2, 102.77} = 8.71$, $P = 0.0003$). However, those numbers did not differ between even and odd years at any site (KA $F_{1, 119} = 1.11$, $P = 0.2936$; YJ $F_{1, 61} = 0.00$, $P = 0.9451$; HN $F_{1, 82} = 0.16$, $P = 0.6886$), suggesting that yearly variations in seed numbers per cone were not correlated with fluctuations in total seed crops. Finally, trees at KA and HN produced cones with more seeds than those at YJ (KA X = 7.2 ± 2.0, N = 121; YJ X = 4.3 ± 1.6, N = 63; HN X = 9.7 ± 1.8, N = 85).

Annual Pattern of dbh Growth

The yearly pattern of increases in tree diameters from 1998 to 2001 was similar across the three sites (Fig. 2). Based on four-year data for all sites, dbh growth was significantly affected by both year and site without the year x site interaction (Table 3). This change in dbh between years was significant for contrasts 1999-1998 and 2001-2000 (Table 4), although the latter became insignificant after a Bonferroni correction. When I considered only the KA trees that were observed for five years, they increased in dbh for every interval except 2000-1999 ($F_{1, 33} = 6.70$, $P = 0.0142$ for contrast 1999-1998; $F_{1, 33} = 1.82$, $P = 0.1866$ for contrast 2000-1999; $F_{1, 33} = 72.55$, $P < 0.0001$ for contrast 2001-2000; $F_{1,33} = 58.22$, $P < 0.0001$ for contrast 2002-2001). Thus, when all three sites were tested together, *P. densiflora* trees tended to or did increase their dbh during even-numbered summers, while those at KA also increased in dbh during Summer 2001.

Annual Pattern of Individual Seed Mass

Mean individual seed mass varied over five years, but without the analogous peaks and troughs recorded for seed-cone crops (Fig. 3A). Overall, the trees at YJ, which had the lowest level of total seed crops of all sites, produced slightly heavier seeds than from trees at KA and HN (KA X = 9.04 ± 2.32 mg, N = 119; YJ X = 11.85 ± 2.49 mg, N = 63; HN X = 10.34 ± 3.01 mg, N = 85). In a nested ANOVA with year, site, and tree identity within sites as main factors, all factors exerted significant effects on seed mass (Table 5). Subsequent two-way ANOVAs for each site

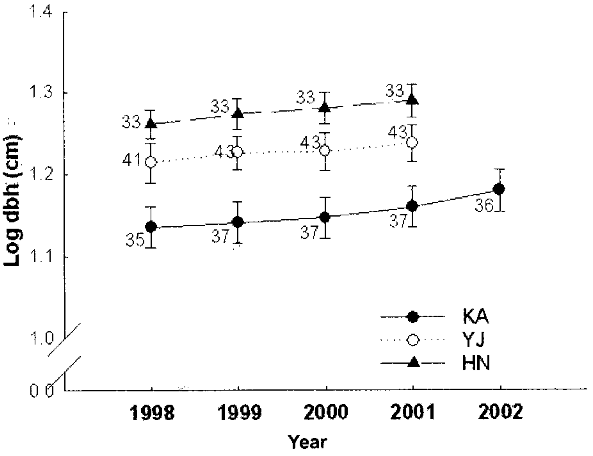

Figure 2. Log of dbh of *P. densiflora* trees measured for four (YJ and HN) and five years (KA). Numbers next to symbols represent sample sizes.

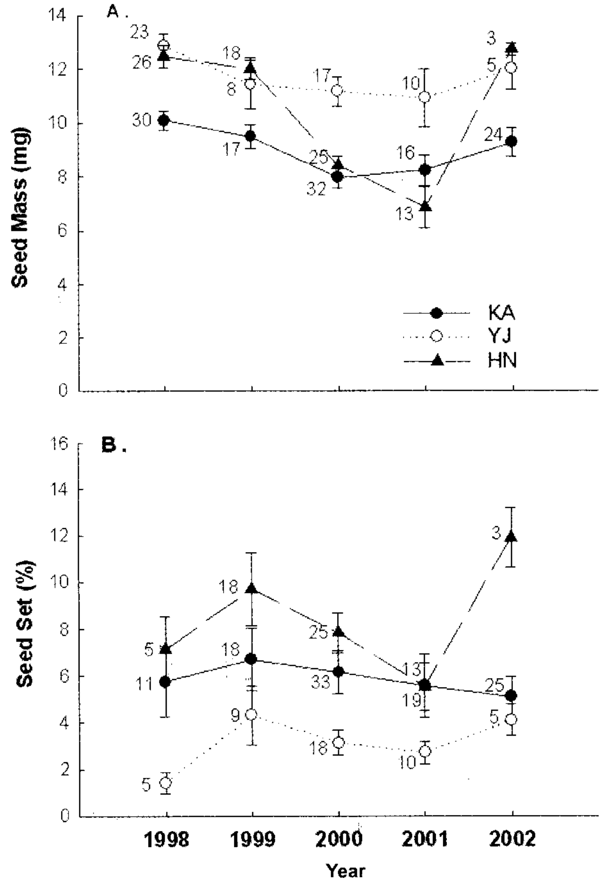

Figure 3. Mean individual seed mass in mg (A) and seed set (B) of *P. densiflora* trees observed for five years at three sites. Numbers next to symbols represent sample sizes.

Table 5. ANOVA on individual seed mass (A) and seed set (B) of *P. densiflora* trees observed over five years at three sites. Analyses were conducted twice for the nested model with site, year, and tree identity within sites as main factors and for the reduced model with year and tree identity as main factors. Total N refers to corrected total N.

	Year			Tree identity (Site)			Site			Total N
	df	F	P	df	F	P	Df	F	P	
A. Seed mass										
Saturated model	4	32.62	<0.0001	93	3.49	<0.0001	2	15.38	<0.0001	268
Reduced model										
KA	4	5.81	0.0004	35	4.90	<0.0001				120
YJ	4	8.22	0.0001	29	5.88	<0.0001				62
HN	4	41.65	<0.0001	29	3.17	0.0002				84
B. Seed set										
Saturated model	4	4.46	0.0021	85	7.24	<0.0001	2	5.70	0.0046	216
Reduced model										
KA	4	1.92	0.1164	34	17.25	<0.0001				105
YJ	4	3.78	0.0190	22	4.89	0.0004				46
HN	4	4.32	0.0071	29	3.58	0.0004				63

also showed that mean seed mass differed among years and trees within sites (Table 5). However, seed mass did not differ between even- and odd-numbered years at any site (KA $F_{1,117} = 0.17$, $P = 0.6830$; YJ $F_{1,61} = 1.97$, $P = 0.1653$; HN $F_{1,83} = 1.24$, $P = 0.2681$).

Annual Pattern of Seed Set

Mean seed set ranged from 4.9% to 7.4% over five years, with only 5.9% of all ovules maturing into seeds (Fig. 3B). Trees at HN had 1.4- and 1.8-times higher probabilities of seed maturation than those at KA and YJ (8.0%, 5.8%, and 3.2%, respectively). All three factors in a nested ANOVA, i.e., year, site, and tree identity within sites, significantly affected seed set (Table 5). In subsequent analyses for each site, seed set differed among years only at YJ and HN (Table 5), although seed set did not differ between even and odd years (YJ $F_{1,45} = 0.40$, $P = 0.5309$; HN $F_{1,62} = 0.02$, $P = 0.8915$).

Annual Pattern of Seed Cone Condition

Most sampled seed cones dehisced (86.9%), while the remaining ones were undehisced, damaged, or stunted in their growth (9.4%, 2.8%, and 0.9%, respectively) (Table 6). Although the association of cone condition and year was highly significant, cone conditions did not appear to vary with even or odd years. For example, the two odd-numbered years, 1999 and 2001, were quite different in terms of their proportions of damaged seed cones, i.e., 0.9% and 13.0%, respectively.

Table 6. Frequency distribution for condition of seed cones collected from *P. densiflora* trees over five years. Dehisced = dehisced cones; Undehisced = undehisced cones; Damaged = cones damaged by seed predators; Stunted = cones stunted in growth.

Year	Dehisced	Undehisced	Damaged	Stunted
1998	594	42	8	0
1999	192	31	2	0
2000	479	92	14	0
2001	170	1	28	17
2002	228	14	1	0
$X^2 = 291.81$, $P < 0.0001$				

DISCUSSION

Pattern of Synchrony

In this study, a large proportion (overall 80.3%) of the *P. densiflora* trees produced seed cones in good years, while at least some (overall 51.6%) produced cones even in bad years. Therefore, strict bimodality of seed cone production did not exist among the trees at all sites. Although these three sites were not exactly congruent over the five years, the general trend was toward an annual fluctuation in cone production that was more or less synchronous within populations that were 17 km to 70 km apart, i.e., even-numbered years being good years and odd-numbered years being poor years. This two-year interval for mast seeding has also been noted for *Pinus resinosa* (Cremer, 1992), but is relatively brief compared with other pines, such as *P. banksiana*, which produce large amounts of seed every four to six years

(Houle and Filion, 1993).

Masting is classified into three groups: strict, normal, or putative (Kelly, 1994). *P. densiflora* is not a strict-masting species because not all trees within a population synchronize their seed cone production in good years. This species also does not appear to undergo putative masting, a phenomenon that is entirely under environmental control, particularly by weather conditions (Kelly, 1994). If *P. densiflora* were more likely to produce massive amounts of seed solely in response to favorable weather, it is expected that weather would be as variable as the pattern of cone cropping across years. However, weather conditions tend to fluctuate less than annual seed production (Koenig and Knops, 2000). Therefore, *P. densiflora*, for which seed production is largely bimodal (i.e., with at least some seed production in poor years), is most likely a normal-masting species.

Annual Pattern of Seed Crops

In *P. densiflora*, even-numbered years (1998, 2000 and 2002) were good seed-crop years. Peaks and troughs in total seed production over the five years were almost consistent across the three sites, which were up to 70 km apart. Thus, the overall 12-fold per-tree increase during good years was a function of the number of trees producing seed cones and the number of cones per tree per year. That the number of seed per cone did not vary between good and poor years is in contrast to results reported by Mencuccini et al. (1995).

Perhaps the most parsimonious explanation for annual fluctuation in seed crops is that masting is a physiological response to the availability of resources. The role of weather conditions, which are assumed to be primary factors that affect photosynthetic rates and, ultimately, resource levels, has been recognized in various conifers and oaks (Lester, 1967; Sork and Bramble, 1993; Mencuccini et al., 1995), but not in other tree species (Sarvas, 1962; Allison, 1990). In the current study, variations in temperature and rainfall were not examined quantitatively from 1998 to 2002 because those five years of observations were not sufficient to allow for quantitative analysis of a possible correlation with seed production. However, it is very unlikely that weather conditions fluctuated to the extent to which annual seed crops did between even and odd years across the three sites. Koenig and Knops (2000) have shown that annual seed crops among species that cover a large geographic area are more variable than weather parameters such as annual rainfall and mean summer temperature. Furthermore, if mast seeding is a response to fluctuations in resources, a high degree of synchrony and bimodality of crops within populations cannot be expected (Koenig et al., 1994). Neither climatic nor edaphic conditions change the overall pattern of mast seeding in *Picea abies*, though the magnitude of annual variations is greater in favorable locations (Mencuccini et al., 1995). Therefore, these previous findings support that mast seeding of *P. densiflora* is likely an evolved phenomenon. Nevertheless, the influence of weather cannot be neglected (Kelly and Sork, 2002).

Evolutionary Mechanism for Mast Seeding

Because tree diameters were measured in late April to early May, their increase from Spring 1998 to Spring 1999 indicated that dbh growth occurred largely between the spring and late summer of 1998. A similar increase in diameter between 2000 and 2001 reflected plant growth during 2000. Thus, by extending the pattern of seed crops during even and odd years, I expect that poor seed crops in 1997 may have led to increased dbh growth from the following Spring to late Summer 1998. If so, these results suggest that mast seeding in a certain year may have depleted the resources needed by *P. densiflora* trees for any significant dbh increase in the next growing season. Conversely, when reproductive costs were low in one year, trees may have been able to increase their dbh the next growing season after a poor seed-production year. However, it must also be mentioned that the trees at KA increased in their dbh during 2001, even after experiencing a good seed year in 2000. Whether this pattern reflected differences in size/age structure or genetic composition among trees at all three sites remains to be tested. The negative effects of reproduction on either subsequent seed production (e.g., Norton and Kelly, 1988; Sork and Bramble, 1993; Koenig and Knops, 2000) or dbh growth (Eis et al., 1965; Koenig and Knops, 1998) are believed to demonstrate an adaptive feature of resource allocation. The potential exists for a negative correlation between reproduction and diameter growth in *P. densiflora*. However, having only five years of data does not permit one to completely evaluate such a trade-off relationship. Therefore, one must assume that the two-year interval for mast seeding from *P. densiflora* is an evolved phenomenon until longer-term data can be accumulated.

Massive flowering increases seed set or seed crops in many wind-pollinated species (e.g., Sarvas, 1955; Nilsson and Wästljung, 1987; Allison, 1990; Sork and Bramble, 1993; Mencuccini et al., 1995; Shibata et al., 1998). Although seed set was low in the pine trees, it varied across the years and, contrary to what was expected, it also greatly fluctuated within even or odd years. Furthermore, unlike in the sizes of their seed crops, the three sites were not similar in their annual patterns of seed set. Thus, *P. densiflora* does not seem to have higher fertilization rates in mast years, behavior that is similar to that reported for three species of oaks in temperate regions (Sork, 1993). However, these current results may not be sufficient to negate the possibility of increased fertilization through mast flowering because the developmental stages of seed cones were not followed here. The abortion of seeds or seed cones in conifer species has been attributed to dry summer weather (Lee, 1979) as well as low fertilization rates (Sarvas, 1962; Owens et al., 1981). In *P. densiflora*, about 90% of the ovules are aborted early, perhaps due to the lack of fertilization (Kang, 1999). The occurrence of stunted seed cones in the current study also implies that the expenditure of resources to seed cones occurred before fertilization. These data strongly suggest that there is room for *P. densiflora* being subjected to selection to improve pollination efficiency. However, to critically test this pollination efficiency hypothesis in relation to mast seeding in that species, one must make direct measurements of fertilization rates in both good and poor crop years (e.g., Smith et al., 1990; Sork, 1993).

Not only seed set but also seed mass and germination ability may increase in mast years. Wardle (1984) and Marchelli and Gallo (1999) have suggested that greater seed mass in mast years implies that the offspring in those years possess a better genetic composition. However, similarly to seed set, there was no indication that seed mass increased in mast years, thereby disproving a possible trade-off relationship between those two parameters. For example, both seed set and mass tended to decrease in 2001, then increase in 2002. Neither was responsive to the size of the seed crops from mast versus non-mast years. This phenomenon might be possible if most of the resources for the seed crops are derived from the cone itself and the adjacent branches. Alternatively, yearly variations in seed mass, which are quite independent of the fluctuations in seed crops, may suggest a statistical limitation caused by small sample size for seed set and mass. However, nested analyses did not consider correlations among years within individual trees. Therefore, repeated-measures analyses should be conducted that allow for variances among years and sites to be removed from the error term.

Pine seeds, which have the highest quality among all tree species, are a food source favored by many rodents and birds (Grodziński and Sawicka-Kapusta, 1970; Smith, 1970). This preference by predators is responsible for the almost complete depletion of such seeds in years of crop failure, as well as the highest predation rate by squirrels on pines, which produce their cones out of synchrony with other trees within populations (Smith, 1970). Squirrels and rats feed heavily, in certain years even devouring up to 100% of the *P. densiflora* seeds in Japan (Rim and Shidei, 1975) and Korea (Park, 2002). Nevertheless, those earlier studies did not distinguish the seed predation rate between mast and non-mast years.

The proportion of damaged seed cones differed greatly between the two poor-crop years; i.e., the predation rate was much higher in 2001 than in 1999. This inconsistency makes it difficult for one to conclude that mast seeding by *P. densiflora* once in two years had evolved to satiate those predators. Nonetheless, this result does not necessarily disprove the seed predation hypothesis because I did not examine the predation rate before seed dispersal. Frugivory by insects, birds, and rodents occurs even when cones are green and undehisced, and different predators exert conflicting selection effects (Nilsson and Wästljung, 1987; Benkman et al., 2003; Siepielski and Benkman, 2004). Thus, future research should involve an investigation of not only the types of predators but also their foraging behavior regarding mast seeding of *P. densiflora* in Korea.

Mast seeding is an important component of plant fitness because it affects the probability of offspring survival and, consequently, the survival of seed dispersers and predators (Nilsson and Wästljung, 1987). However, the impact of mast seeding, including mast flowering, on animals in natural populations has rarely been quantified (Herrera et al., 1998). Although annual fluctuations in the production of seed crops has long been studied, most research projects, similarly to the one presented here, have failed to obtain results that could support only one of the two alternative hypotheses (e.g., Norton and Kelly, 1988; Koenig and Knops, 1998; Shibata et al., 1998; reviewed in Kelly and Sork, 2002). Therefore, longer-term studies are required that consider how events during a plant's life, such as flowering and fruiting, might be correlated somehow, and affect the cyclic pattern of mast-seeding. In addition, it will be useful to analyze the vectors involved in pollination, seed predation, and seed dispersal, to completely understand how the incidence of mast seeding develops.

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LITERATURE CITED

Allison TD (1990) Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. Ecology 71: 516-522

Bawa KS (1980) Evolution of dioecy in flowering plants. Annu Rev Ecol Syst 11: 15-39

Benkman CW, Parchman TL, Favis A, Siepielski AM (2003) Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. Amer Nat 162: 182-194

Bossema I (1979) Jays and oaks: An eco-ethological study of a symbiosis. Behavior 70: 1-118

Caron GE, Powell GR (1989) Patterns of seed-cone and pollen-cone production in young *Picea mariana* trees. Can J For Res 19: 359-364

Cremer KW (1992) Relations between reproductive growth and vegetative growth of *Pinus radiata*. For Ecol Manage 52: 179-199

Eis S, Garman EH, Ebel L (1965) Relation between cone production and diameter increment of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco.], grand fir [*Abies grandis* (Dougl.) Lindl.], and western white pine (*Pinus monticola* Dougl.). Can J Bot 43: 1553-1559

Grodziński W, Sawicka-Kapusta K (1970) Energy values of tree-seeds eaten by small mammals. Oikos 21: 52-58

Herrera CM, Jordano P, Guitián J, Traveset A (1998) Annual variability in seed production by woody plants and the masting concept: Reassessment of principles and relationship to pollination and seed dispersal. Amer Nat 152: 576-594

Hong SK, Rim YD (1997) Effect of mosaic vegetation structure on pine seed predation by forest animals in agricultural landscape. Kor J Ecol 20: 265-274

Houle G (1999) Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. J Ecol 87: 413-422

Houle G, Filion L (1993) Interannual variations in the seed production of *Pinus banksiana* at the limit of the species distribution in Northern Quebec, Canada. Amer J Bot 80: 1242-1250

Janzen DH (1971) Seed predation by animals. Annu Rev Ecol Syst 2: 465-492

Kang H (1999) Variations in the seed production of *Pinus densiflora* trees. Kor J Biol Sci 3: 29-39

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9: 465-470

Kelly D, Sork VL (2002) Mast seeding in perennial plants: Why, how, where? Annu Rev Ecol Syst 33: 427-447

Koenig WD, Knops JMH (1998) Scale of mast-seeding and tree-ring growth. Nature 396: 225-226

Koenig WD, Knops JMH (2000) Patterns of annual seed production by northern hemisphere trees: A global perspective. Amer Nat 155: 59-69

Koenig WD, Mumme RL, Carmen WJ, Stanback MT (1994) Acorn production by oaks in central coastal California: Variation within and among years. Ecology 75: 99-109

Lee KJ (1979) Factors affecting cone initiation in pines: A review. Inst For Genet Res Rep 15: 45-85

Lester DT (1967) Variation in cone production of red pine in relation to weather. Can J Bot 45: 1683-1691

Lloyd DG (1984) Gender allocations in outcrossing cosexual plants. *In* R Dirzo, J Sarukhan, eds, Perspectives on Plant Population Ecology. Sinauer, Sunderland, pp 277-300

Mäkinen H (1998) The suitability of height and radial increment variation in *Pinus sylvestris* (L.) for expressing environmental signals. For Ecol Manage 112: 191-197

Marchelli P, Gallo LA (1999) Annual and geographic variation in seed traits of Argentinean populations of southern beech *Nothofagus nervosa* (Phil.) Dim et For Ecol Manage 121: 239-250

Mencuccini, Piussi MP, Sanzi Sulli A (1995) Thirty years of seed production in a subalpine Norway spruce forest: Patterns of temporal and spatial variation. For Ecol Manage 76: 109-125

Nilsson SG, Wästljung U (1987) Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. Ecology 68: 260-265

Norton DA, Kelly D (1988) Mast seeding over 33 years by *Dacyrdium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: The importance of the economies of scale. Funct Ecol 2: 399-408

Owens JN, Simpson SJ, Molder M (1981) Sexual reproduction of *Pinus contorta*. I. Pollen development, the pollination mechanism, and early ovule development. Can J Bot 59: 1828-1843

Park JK (2002) Animal behaviours related to pine seeds on the forest floor. Kor J Ecol Sci 1: 79-82

Rim YD, Shidei T (1975) Animal influences on Japanese pine seeds of the forest floor. II. Seed input and output of seedlings with seed coat. Jap J Ecol 25: 141-148

Sarvas R (1955) Investigations into the flowering and seed quality of seed crop. Commun Inst For Fenn 45: 1-37

Sarvas R (1962) Investigations on the flowering and seed crop of *Pinus sylvestris*. Commun Inst For Fenn 53: 1-198

SAS (1999) SAS User's Guide: Statistics. SAS Institute, Cary, USA

Schoen DJ, Stewart SC (1986) Variation in male reproductive investment and male reproductive success in white spruce. Evolution 40: 1109-1120

Sharp WM, Sprague VG (1967) Flowering and fruiting in the white oak pistillate flowering, acorn development, weather, and yields. Ecology 48: 243-251

Shibata M, Tanaka H, Nakashizuka T (1998) Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. Ecology 79: 54-64

Siepielski AM, Benkman CW (2004) Interactions among moths, crossbills, squirrels, and lodgepole pine in a geographic selection mosaic. Evolution 58: 95-101

Silvertown JW (1980) The evolutionary ecology of mast seeding in trees. Biol J Linn Soc 14: 235-250

Smith CC (1970) The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol Monogr 40: 349-371

Smith CC, Hamrick JL, Kramer CL (1990) The advantage of mast years for wind pollination. Amer Nat 136: 154-166

Sork VL (1993) Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *In* T Fleming, A Estrada, eds, Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects. Kluwer Academic Publishers, Dordrecht, pp 133-147

Sork VL, Bramble J (1993) Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 74: 528-541

Tappeiner JC (1969) Effect of cone production on branch, needle, and xylem ring growth of Sierra Nevada Douglas fir. For Sci 15: 171-174

von Ende CN (2001) Repeated-measures analysis. *In* SM Scheiner, J Gurevitch, eds, Design and Analysis of Ecological Experiments. Oxford University Press, New York, pp 134-157

Wardle JA (1984) The New Zealand Beeches: Ecology, Utilization and Management. New Zealand Forest Service, Wellington