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 mature 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