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Delayed Seed Dispersal in *Pinus torreyana* (Torrey Pine)

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Summary. Torrey pine exhibits a pattern of seed release intermediate between an open and closed-cone species. It was found that the cones open at maturity, but that seed fall from some cones continues for up to 13 years. Approximately 77% of the total seed crop was present in age classes one or more years past the time of seed maturity.

Serotiny is thought to evolve in response to fire, and partial serotiny at the population level has been attributed to circumstances in which the strong selective pressure of fire is relaxed. We hypothesize that delayed seed dispersal in Torrey pine is a stable trait which is the result of a pattern of large relatively rare crown fires separated by intervals longer than one generation. The reduced serotiny observed in other conifers on headlands and islands in California seems consistent with our hypothesis.

Introduction

Cone serotiny in conifers has evolved in response to fire. Retention of seeds in closed cones provides species which are fire sensitive and have little capacity for resprouting with a means of leaving offspring after crown fires. There can be little doubt that the trait is derived from the open-cone condition and although Shaw (1914) felt that closed-cone pines were closely related, it seems more likely that the trait has appeared independently in different lineages (Duffield 1952).

Detailed work on cone serotiny in *P. contorta* supports the view that serotiny is a flexible trait subject to selection. Lotan (1967, 1968, 1976) and Perry and Lotan (1979) have shown that populations of this species differ in degree of serotiny. It appears these differences are explainable on the basis of geographical and historical variation in fire pattern.

The Mediterranean climate zone along the Pacific Coast of North America is subject to extensive crown fires, and it is not surprising that some of the most extreme examples of cone serotiny are to be found there. *Pinus attenuata* (Vogl 1973) and some populations of *P. muricata* (Duffield 1951) both retain unopened cones for twenty years or more. Cone opening except after fires is sporadic and ineffectual in dispersing seeds. The value of this trait in surviving wildfire has been clearly documented (Vogl 1973, Zedler 1977).

Torrey pine (*P. torreyana* Parry ex. Carr), a California species which is widely planted but which has only two natural stands of very limited extent, seems to be an anomaly. On the assumption that pine species adjust the degree of serotiny to the prevailing fire climate, it would be expected to be a closed-cone species. Its mainland stand in San Diego County is in an ecological setting not obviously different from that occupied by strongly sertotinous *P. muricata* populations to the north in Santa Barbara County, and to the south in Baja California, Mexico. But the literature suggests that Torrey pine cones are not serotinous. Sudworth (1908) reports that the cones open at maturity, but he and others (e.g. Shaw 1914) also state that the open cones are retained on the tree for many years. There is uncertainty if Torrey pine should be grouped with the other California coastal conifers (about 4 species of *Pinus* and 6 species of *Cupressus*) which clearly show closed-cone behavior (Vogl et al. 1977).

This study was undertaken to determine the seed retention characteristics of Torrey pine. There were two main objectives: 1) to predict how Torrey pine might react to wildfires or controlled fires of different kinds, and 2) to improve our understanding of cone serotiny in conifers of the Pacific Coast.

Methods

Data were collected in the Torrey Pine State Reserve in the summer and fall of 1978. To minimize damage to the stands, cones were collected only from windfallen trees and from trees whose crowns could be reached by a truck-mounted ladder. All cones were removed from the 15 windfallen trees. On other trees all cones were taken from major branches from the branch tip to the main bole. A total of 804 cones were collected, 67% of which came from the standing trees. The age of the cones was estimated at the time of collection by counting the bud scale scars back from the tip of the branch (Badran 1949, Harlow 1959).

In Torrey pine the cone bases remain when the cone is shed. The presence of these cone remnants was noted during sampling and used to estimate the onset of cone shedding.

Torrey pine cones are pollinated in late winter (from January to March) and reach maturity in late winter about two years after pollination. For simplicity the data are grouped by age classes, where the year class is the truncated true age at the time of the summer and fall collections in 1978 measured from the usual time of pollination. For example, the one year class contains cones that were pollinated about one and half years before the time of collection and the two year class contains cones that were just mature at the time of collection.

After collection the cones were stored at room temperature until dissected. Before dissection the degree to which the cones had opened was determined visually by estimating the percent of cone scales that had separated enough to permit dispersal of the enclosed seeds. Thus a cone estimated to be 50% open would be expected to have lost about half of its seeds. No evidence of cone opening during storage was observed.

Germination trials were conducted in December 1978 on stratified and nonstratified seeds. Stratified seeds gave the highest germination

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rates and those data are used in discussing viability estimates. Seeds were stratified for 43 days at 3° C and germinated in petri dishes in a temperature controlled chamber in the dark with temperature regime of eight hours at 20° C and sixteen hours at 10° C. Captan was added to control fungi. Sample sizes for the germination tests varied between 17 and 138 seeds. A seed was considered to have germinated if it produced a radicle at least 3 mm long.

Results

Torrey pine cones mature in the third year (age class 2) but the frequency distribution of cone age shows that some cones are retained up to the fifteenth year after maturity (Fig. 1 A). Older cones are a significant proportion of the cone population. Those beyond the eighth age class accounted for 15% of the total sample.

It was noted at the time of collection that no fully formed cones were shed in the first three age classes. This means that most of the variation in numbers of cones up to the fourth year class is due to variable cone production. Beyond this age the shape of the curve suggests an exponential decline. A linear regression of the log of relative cone frequency against cone age class for classes 3 through 15, taking an average of the first three values for the class three value, is highly significant ($r^2=0.88$, $p<0.001$).

Visual estimates showed that cone opening begins at cone maturity and continues gradually over a period of years. The data (Fig. 1 B) are combined because all individuals sampled, and indeed all Torrey pines in the reserve, show a qualitatively similar pattern of cone opening. Unlike *P. contorta* (Perry and Lotan 1979), *P. torreyana* populations show no evidence of polymorphism with respect to serotiny.

On the average, about 38% of the scales open enough to permit seeds to fall when the cone matures at about $2\frac{1}{2}$ years (i.e. enters the 2 year class, Fig. 1 B). This percentage rises steeply to 75% in the next two age classes and then increases gradually. Because of this gradual opening, a significant proportion of the seeds are retained in cones past maturity.

A seed depletion curve (Fig. 1 C) was calculated by expressing the average number of total seeds per cone for each age class as a proportion of the average number of total seeds in unopened cones ($\bar{X}=82.9$ seeds/unopened cones). Seed loss is initially high, but declines sharply beyond the fourth age class. A linear regression on the points beyond the first two age classes is significant ($r^2=0.67$, $p<0.001$). The seeds in the basal (proximal) scales are the last to fall, and in the oldest cones few seeds are found in the upper or middle portion of the cone.

A frequency distribution of the proportion of the total seed crop in each age class (Fig. 1 D) shows that age class 3 contains almost 30% of the seeds, a consequence of the heavy cone production in that year. The shape of this distribution results both from the average rate of seed loss with time and from year-to-year variation in cone and seed production. The same curve for the previous year (1977) would have had an even more pronounced peak at year class 2 when the very large three year class of cones was newly mature.

Because the seeds are retained in partially open cones it might be expected that they would rapidly lose viability from insects, pathogens, and physical weathering. Inspection of the seeds revealed that 6.8% of the total sample had visible insect damage, but there was no statistically significant relationship with cone age. If major insect damage occurs, it probably happens early in cone development.

Viability, as assessed by the proportion of empty seeds (Fig. 2 A) and by germination tests on stratified seeds (Fig. 2 B) did, however, decline significantly with cone age. The increase in the proportion of empty seeds with time simply may be the result of differential loss of full and empty seeds; but germination of the remaining filled seeds declines with increasing cone age. It is initially low in the mostly immature seeds in the cones of the first year; rises to a maximum in the newly mature cones, and then declines with much variability but an approximately linear trend (Fig. 2 B). It is remarkable that seeds at least partially exposed for ten years remain viable. This can be attributed to the heavy seedcoat of Torrey pine and the mild and dry climate.

An unusual cause of pre-dispersal loss of seeds is germination

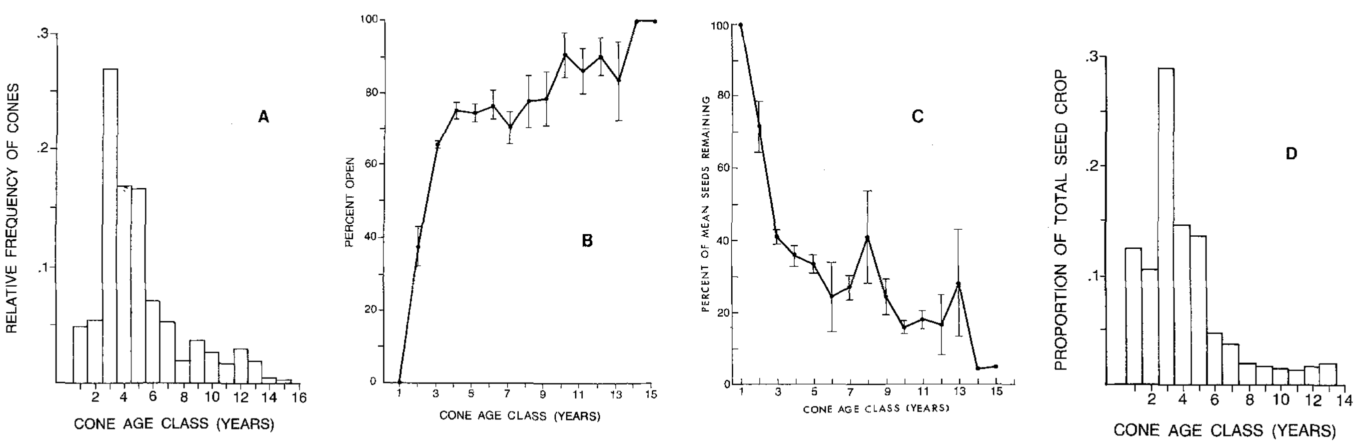

Fig. 1. A Age distribution of cones sampled during the summer of 1978. Cones were collected from standing and windfallen trees. Each age class represents the truncated true age at the time of collection measured from the usual time of pollination. **B** The mean estimated percent of opened cone scales per cone age class. The degree of cone opening was determined visually. Standard error bars (±1 SE) have been omitted for the 14 and 15 years classes due to their small sample sizes. **C** The relation between cone age and the mean percent of total seeds remaining within the cone (±1 SE bar). Cones were collected and manually opened to obtain the contained seeds. This number was then contrasted to a mean of 82.9 seeds in an unopened cone. Standard error bars were omitted for the 14 and 15 years classes due to their small symple sizes. **D** The percent each age class contributes to the total seed crop in the sampled stand. Sampled cones were manually opened to determine the total number of seeds for each age class. This value was then divided by the total number of seeds for all classes

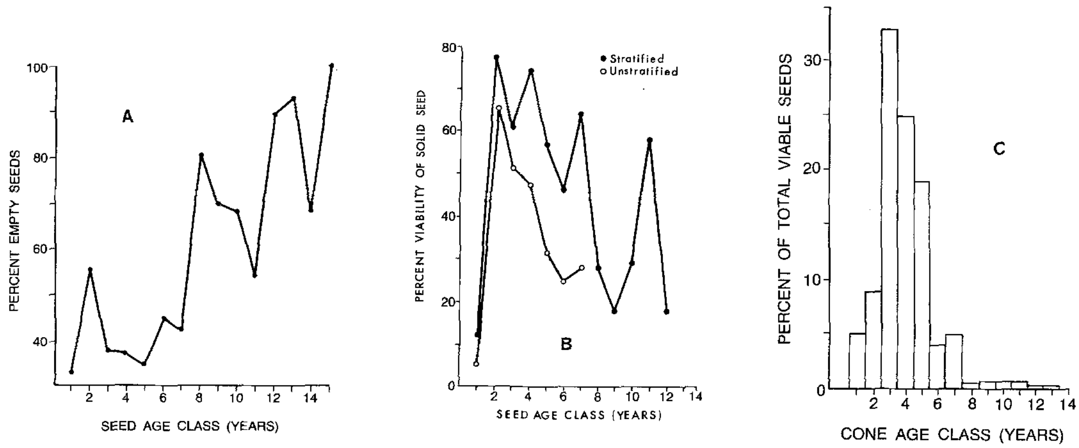

Fig. 2. A The percent of seeds for each age class that are empty. Empty seeds were determined by cutting open seeds from collected cones. **B** Viability of stratified and unstratified solid seeds by age class. Viability results are from germination tests. One year age class seeds were still germinating at 139 days when the trials were completed; this presumably was due to after-ripening. **C** Percent of viable seeds contributed by each age class to the total number of seeds viable on the tree. Viability was determined by germination tests. Germination of seeds in the one year class is presumably due to the maturation of the seeds following collection of the cones

in the cone. This maladaptive vivipary, apparently unique in the genus to Torrey pine, is readily detected by the presence of a seedling associated with a split seed. For the entire sample, 4.6% of the seeds were found to have germinated in the cone, with a peak in year class 4. There was no correlation with cone age. These seeds germinated in the winter of 1977–1978 when rainfall was exceptionally high. The average rate of loss from this cause is probably less than this sample indicates.

The information on viability, soundness, seeds per cone, numbers of cones, and other sources of loss can be combined to show relative contribution of each age class to the effective seed crop on the trees at the time of the sample (Fig. 2C). The population of viable seeds on the trees is primarily in the 3, 4, and 5 year classes, with only a small proportion in year classes beyond 7. Although this frequency distribution will vary from year to year because of varying cone production (Fig. 2C) it is clear that older cones in most years would retain significant numbers of seeds.

Discussion

Torrey pine cones show a marked tendency towards delayed seed dispersal and although in a literal sense it is not a closed-cone species it has the potential to function as one. At the time of our sample, over 76% of the available seeds were in cones one or more years past maturity. While there is no way to rule out completely the possibility that seed retention in Torrey pine is a chance pattern of no adaptive value, the obvious advantage of serotiny to other pines and cypresses that grow under similar conditions make it reasonable to suppose that delayed dispersal by Torrey pine can be explained by the ecological setting in which it has evolved.

Field observations on the response of Torrey pine to fire are limited because fire control has been strict in the State Reserve for the last 50 years. But in 1972 a hot fire set by an arsonist killed all of the Torrey pine trees in about 8 ha of the State Reserve. Seedling establishment was observed in the first growing seasons after the fire, and a substantial number of these survived. In 1979, 220 saplings and seedlings were counted in the area of the 1972 fire where 93 trees had been killed, suggesting a possible long-range increase in density (McMaster 1980). Seedlings and saplings were absent in an adjacent unburned area.

Seedling establishment also occurs without fire. A survey of ten areas (about 20,000 m^2 total) in the State Reserve revealed 46 seedlings in the period January 1978 to June 1979 (McMaster 1980). By June 1979 only 25 of these seedlings were still alive. The presence of a few saplings in areas not burned in the last 50 years and the uneven-age structure of some local populations is evidence that seedlings established without fire do survive to maturity.

In interpreting the observed pattern of seed retention in Torrey pine, the main problem is to explain how its seemingly anomalous pattern of gradual seed release can be advantageous, or alternatively, how it could arise even if it were not advantageous. It will be assumed in the discussion that three qualities of fire are of critical importance: 1) the proportion of the population within the fire area killed by the fire, an intense crown fire being one which causes virtually complete mortality, 2) the length of time between fires, and 3) the extent and spatial pattern of fires, particularly the size of burns relative to dispersal ability.

The extreme of closed-cone behavior like that found in *P. attenuata* and some populations of *P. muricata* is expected when fires burn all aboveground plant material over wide areas and are separated by intervals shorter than the average life expectancy of individuals that reach reproductive age. Under these conditions, seeds dispersed between fires would have only a small probability of producing a reproductive plant before the next fire, and the open-cone trait would be of little advantage. Because of large fire size, open-coned survivors in adjacent areas would make minimal contributions to the next generation of trees, and future fires would have a high probablity of eliminating them and their descendants. If Torrey pine evolved under a fire regime of this kind its present pattern of seed retention would have to be explained as an imperfect approximation to the more suitable closed-cone condition.

If a fire regime is characterized by less intense, very small, or very rare fires, the closed-cone is no longer advantageous (Perry and Lotan 1979). Open-cone trees can establish seedlings that have a good prospect of leaving descendents while closed-cone trees would be retaining seeds for a crown fire that has a small probability of occuring within their lifespan. If Torrey pine evolved under a fire regime of this kind, delayed seed dispersal would again seem to be a sub-optimal trait that is either not subject to selection or is in the process of change.

It may be that the cones are as close to complete serotiny as possible given the genetic constraints, and that the natural distribution of Torrey pine is restricted partly because of its incomplete adaptation to fire. The two species most closely related to Torrey pine, *P. coulteri* and *P. sabiniana*, show tendencies toward delayed dispersal (J. Griffin and W. Critchfield pers. comm 1979, Griffin 1962) and retain some cones following maturity (Munz and Keck 1973). It may then be that delayed seed dispersal is a fixed character in this group, present because of its inheritance from a common ancestor. Because *P. coulteri* and *P. sabiniana* also frequently experience fire, it may also be that similar seed retention patterns evolved in response to a similar fire climate.

However, it is not necessary to assume either sub-optimality or active evolution. Partial serotiny can be explained by random variation in the extent and intensity of fire. Intense crown fires that occurred only occasionally could still exert very strong selective pressure against individuals that retained no viable seeds, especially when cone production is also characterized by large year-to-year variation. If cone production were consistently high, and fires occurred before seeds were shed in the fall and winter, the current cone crop might be a sufficient hedge against crown fires. But with high variability in cone production trees could be burned in a year of low seed availability. Our observations showed that in 1978 the two year old cone crop was small, and the cones older than the newly mature two year old cones contained about 85% of the total viable seeds on the tree. Seed retention averages out the year-to-year variation in seed production and insures that for most individuals at least some seed will fall after a fire.

If the crown fires were separated by intervals long enough to permit the establishment of individuals that can themselves reach reproductive age before the next fire, there would be an advantage to dispersing seeds as soon as cones mature. This could counterbalance the strong selection by crown fires. Observations have confirmed that seedling establishment in unburned stands does occur, although the number of saplings is small in comparison to the adult densities (McMaster 1980). Thus long intervals between fires could be exploited by individuals that disperse seeds at cone maturity. It may be that the partial serotiny of Torrey pine is an evolutionary compromise resulting from the alternation of episodes selecting strongly for and against serotiny. In ecological terms it is analogous to other germination and dispersal mechanisms which hedge against environmental variation, such as seed dimorphism (van der Pijl 1972, Baker and O'Dowd in press).

The spatial pattern of fires is also important. For serotiny to be advantageous and persist, the average size of catastrophic fires must be large enough to make dispersal of seeds from adjacent unburned areas insignificant in reestablishment. If there is substantial input from trees on the margins of burns, the next generation of trees in the area of the catastrophic burn could include a high proportion of individuals descended from open cone progenitors, and the relative advantage of serotiny would be small or nonexistent. Since Torrey pine seeds are large and heavy, fire size need not be very large for dispersal from unburned areas to be unimportant. While the broken topography in which the species occurs would tend to favor a small-scale mosaic, the majority of trees occur with highly flammable chaparral and coastal sage scrub species that can readily carry fire.

This hypothesis to explain the survival value of delayed seed dispersal is supported by the patterns of serotiny seen in the other coastal conifers in California when these are examined in detail. The most strongly serotinous pines and cypresses occur on the mainland and in association with dense and continuous areas of chaparral and coastal and inland sage (Griffin and Critchfield 1972). On the islands and in stands that occur on headlands, coastal bluffs, and dunes, serotiny is much less pronounced. This pattern is shown by the Oocarpae sub-section of pines (Critchfield and Little 1966), consisting of *P. attenuata*, *P. radiata, P. muricata,* and the doubtfully distinct *P. remorata*. The most strongly serotinous populations are *P. attenuata* and the mainland populations of *P. muricata*. The most strictly coastal of these species *P. radiata*, while definitely serotinous, has cones which can open readily on hot summer days and commonly bears many open cones. (J. Griffin pers. comm.). *P. remorata*, which occurs primarily on the California channel islands, also has cones that remain closed for only a few years.

Similar trends are apparent in *Cupressus*. *C. macrocarpa*, which is confined to headlands, occurs in a ecological setting very similar to that of Torrey pine. Its cones remain closed for only a few years, and seed dispersal is a continuous process. Like Torrey pine, it seems to have an intermediate strategy, capable of surviving with or without crown fire. In contrast, species of cypress with a more inland distribution (e.g. *C. forbesii*, *C. sargentii*) are strongly serotinous. Unless disturbed by man, the stands are even aged, and have little tendency to establish seedlings except after fire. (Vogl et al. 1977, Zedler 1977, in press).

The geographical pattern of cone serotiny suggests that in the immediate vicinity of the ocean there is a reduced frequency of intense crown fires. The often dense shrub vegetation along the coast has fuel characteristics very similar to that of the vegetation found in association with more inland conifers, but the maritime influence and local topography presumably reduces the probability of fire. A lower probability of fire in any one year would lead to the buildup of plant biomass, making the crown fires very intense when they do inevitably occur.

We hypothesize that the delayed seed dispersal of Torrey pine and the reduced serotiny of other coastal and insular conifers arise from the same cause: a fire pattern in which large scale intense crown fires alternated with long intervals in which there either were no fires at all, or in which there were only light surface fires.

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