The Fire Pines

by RICHARD WARREN and ALFRED J. FORDHAM

Author's Note: When an Arnold Arboretum volunteer develops an interest in conifers, he inevitably comes under the stimulating influence of Alfred Fordham. So it happened with me. One day Al remarked on a photograph he had taken of *Pinus attenuata*. The branches were covered with closed cones all the way back to the tree trunk. The conversation then led to the question of how long seeds can remain viable in these cones. Since no answer was easily discovered in reference books, we decided to inquire more deeply. This we did by consulting source material in libraries, writing letters to various experts, and performing our own tests of seed germination in the Dana Greenhouses.

The most consistently serotinous pines, *Pinus radiata* and *P. attenuata*, are not hardy in the Arboretum. I have, however, enjoyed the privilege of frequent trips to Western Ireland where *P. radiata* is planted as a shelter from the high winds of the area. Also, fortunately, a daughter in Marin County, California, lives within an easy drive of the dry elevations of the coastal range where *P. attenuata* thrives. Material for this inquiry was obtained from these sources. (R.W.)

Among the most interesting members of the pine genus are those to which we apply the term "serotinous." The word means "late developing" and describes their distinguishing feature, the habit of holding cones closed on their branches for many years. A strong resin glues the tips of the scales together and these trees do not disperse their seeds at maturity as other pines do. In many cases seeds are not liberated until a forest fire melts the resin; hence the common name, "Fire Pines." Subsequent revegetation of the burned area is of teleological significance for the survival of the species.

Table I lists these pines. The degree to which they demonstrate serotinous tendencies varies between species, and in some of these also according to geographic location. Variation may be seen both in the proportion of cones with persisting closure and in its duration. In some trees of *Pinus banksiana, P. clausa, P. rigida* and *P. contorta*, for instance, the cones open at maturity. This seldom occurs in *P. serotina*, but later separation of scales and seed dispersion almost always occurs before five years. *P. radiata* plants in the British Isles, furthermore, hold their cones closed for a long period, but in California in exposed sunny positions they may open a year or two after ripening. Badran observed that *P. radiata* from the Monterey Peninsula showed many open cones, particularly those that were more than four years old, whereas those from most specimens found in the Berkeley-Oakland Hills area remained closed. *P. contorta*

TABLE I
SEROTINOUS PINES

West Coast U.S.A.	
P. attenuata	Knobcone Pine
P. contorta	Beach Pine
P. muricata	Bishop's Pine
P. radiata	Monterey Pine
Rocky Mountains U.S.A.	
P. contorta var. *latifolia*	Lodgepole Pine
Canada and Northern U.S.A.	
P. banksiana	Jack Pine
Eastern U.S.A.	
P. pungens	Table Mountain Pine
P. rigida	Pitch Pine
Southern U.S.A.	
P. clausa	Sand Pine
P. serotina	Pond Pine
Mexico	
P. greggii	Gregg's Pine
P. oocarpa	No common name
P. patula	Spreading-Leaved Pine
P. pringlei	Pringle's Pine
Mediterranean	
P. halepensis	Aleppo Pine
P. pinaster	Maritime Pine

also demonstrates the influence of climate on the serotinous habit. The cones of plants in coastal regions open promptly, whereas those in the Rocky Mountain and Intermountain regions are persistently serotinous. Cones of *P. attenuata* are virtually unknown to open under influences other than fire, decay, or attack by wildlife or insects. This persistence may be the result of its restricted geographical distribution in the California coastal mountains. Genetic factors also seem to play a part (Fig. 1).

The retention of cones by serotinous pines even after opening is characteristic. In the New England area it is familiar to us in the cone-peppered silhouettes of *Pinus rigida,* and in Canada of *P. banksiana.*

The relation between the cone and the branch on which it remains is of note. In the specimens of *Pinus radiata* we have observed, the cones most recently matured have had pedicels of 1 cm. As the branch has grown in diameter, the pedicels have been swallowed so that by the third or fourth year the cones have become sessile. In cones up to thirty years of age, the pedicel has continued to stretch and their bases have remained tightly pressed against the branch. In other species such as *P. banksiana* and *P. attenuata*, however, the woody tissues have been observed to grow out around the cone

Fig. 1. Closed cone characteristics can vary from tree to tree in the case of Pinus banksiana. *At right is a specimen collected from a tree where some cones were closed and some were open. Below is one in which all cones are closed. Both trees were siblings grown together in a nursery row. Still other plants in the same population had cones that were all open. These characteristics are genetic, and it is not uncommon to see trees in native habitats whose cones are all serotinous growing beside trees with cones all open and still others that contain some of each. Photos: A. Fordham.*

so that it becomes embedded and actually disappears within the wood (Figs. 2 and 3). Why this occurs in some species and not in others is unknown. Coker suggests that it is pure mechanics, the breadth of the surface presented to the branch being less in the narrower cones of *P. attenuata* and *P. banksiana* than in the broader ones of *P. radiata* and *P. muricata.*

The degree to which advancing age of cones may influence the germinating ability of seeds should be of particular interest to the Arnold Arboretum since Professor C. S. Sargent seems to have been among the first to ask the question. He received a branch of *Pinus contorta* from Dr. George Englemann (Fig. 4) four and a half years

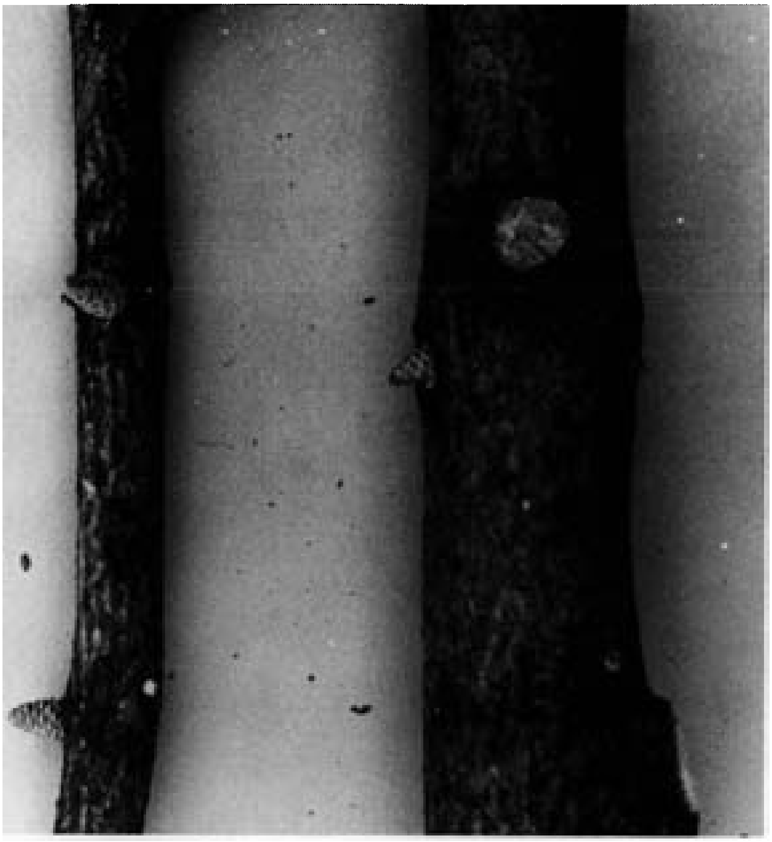

Fig. 2. Cones of Pinus banksiana *in various stages of embedment. Sister trees in the same nursery row did not engulf their cones as did this one. Photo: A. Fordham.*

Fig. 3. A transverse section of a Pinus banksiana *tree trunk, from the same tree that provided Fig. 2. It was collected at a 5-foot level from a fast growing tree in a nursery row and shows nine annual growth rings. The embedded cone is one of a pair that originated nine years ago at the tip of a shoot that was about 1/4-inch in diameter. As the trunk increased in girth during the first four years, the cone was forced outward and this caused the pedicel to elongate. Wood that formed during the fifth annual growth increment surrounded the cone and this process continued each year until only the tip remained uncovered after the 1976 growing season. In the course of another year, it seemed probable that it would have been completely hidden and the sound seeds it contained would then be lost for reproduction.*

Cones of Pinus banksiana *often appear in multiples of two and three. This illustration shows one of a pair that continued to grow, and evidence of one that failed six years ago. The annual rings show that at that time the cone was entirely exposed (not embedded at all) and may have been destroyed by a squirrel seeking seeds. It is interesting to see how annual growths have filled the void. Photo: A. Fordham.*

after it had been collected from a tree in Colorado in 1874. Five years later, on planting the seeds, he observed germination for the years 1869 through 1872, but not for 1873, the most recent year, nor for the earlier years of 1865 and 1868. He commented that "this experiment is unsatisfactory owing to the want of seeds of 1866 and 1867 and because those of 1873 had probably never fully developed. It is only interesting in view of the fact that it may possibly lead to this subject being more fully investigated. It is particu-

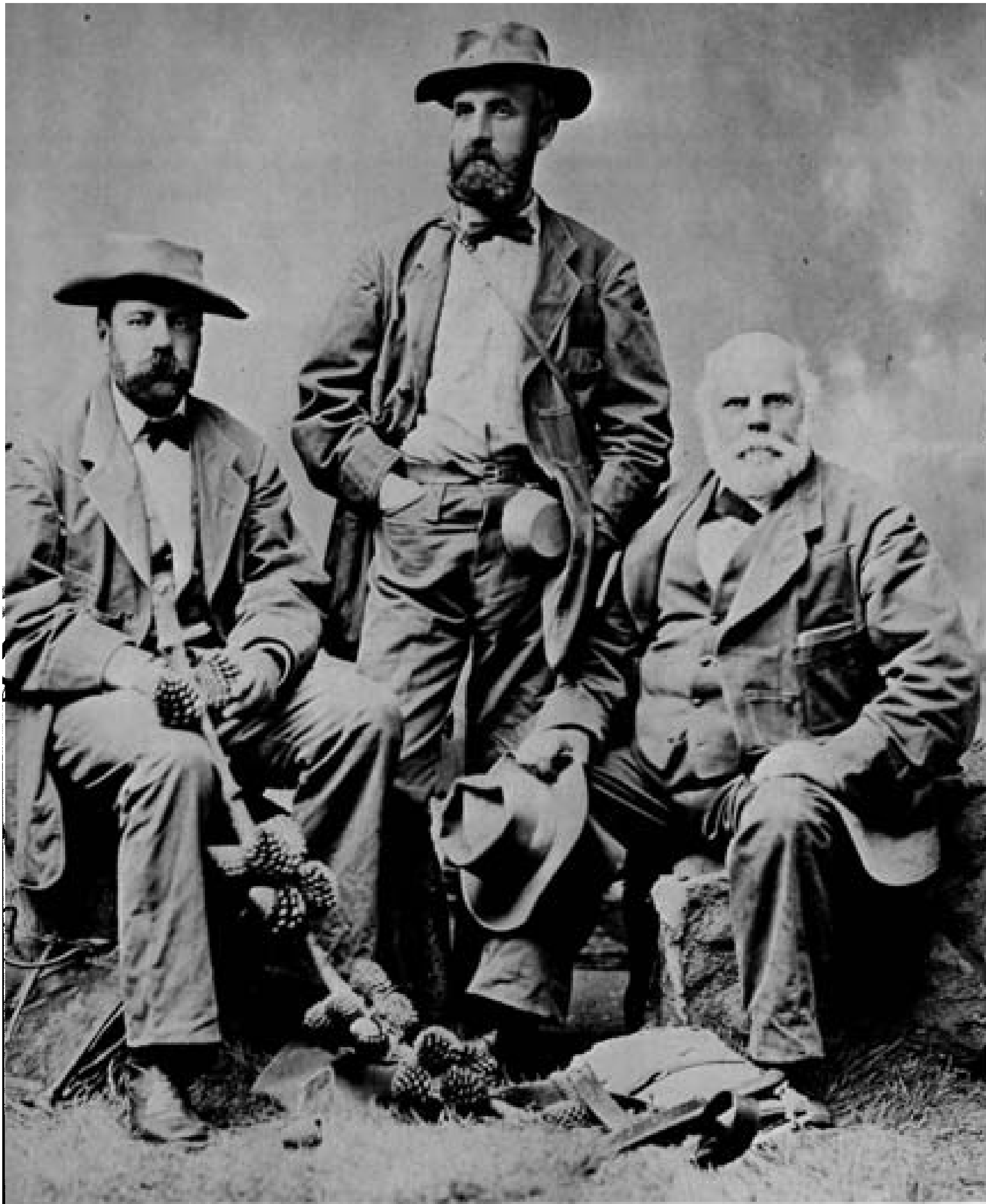

Fig. 4. Charles S. Sargent, Francis Skinner and George Englemann posed in Monterey, California, in 1880 toward the end of their summer trip in connection with the U. S. forest census. Note that some of the cones on the branch Sargent is holding are open and some are closed, a normal occurrence for Pinus radiata *in coastal areas (see text).*

larly desirable to obtain and test the seeds from old serotinous cones of such species as *P. serotina*, the Florida Pine, *P. inops* var. *clausa* (*P. clausa*) *, *P. Tuberculata* (*P. attenuata*) *, *P. muricata*, and *P. insignis* (*P. radiata*) *. There are always facilities for making such experiments at the Arboretum when sufficient material can be obtained."

Although throughout the world much effort has been put into investigating methods to increase the yield of seeds of serotinous pines for forestation purposes, little attention has been devoted to answering Sargent's question: How long *can* the seeds remain viable in the cones? Now, nearly one hundred years later, we have used the Arboretum's facilities to test the influence of age on germination of seeds of cones from *Pinus radiata* collected in West Cork, Ireland. The following discussion will tell us of this experiment together with what we have been able to discover of others.

In 1909 Professor W. C. Coker of the University of North Carolina procured cones of *Pinus serotina* up to fourteen years old and germinated seeds from all years. Badran in 1949 observed germination of seeds of *P. radiata* from cones up to ten years old, and of *P. attenuata* from those up to twenty years old. Other allusions to the very long viability of seeds are Bowers, fifty years; Kotok, eighty years; Mason, seventy-five to eighty; and Mills, one hundred fifty — all for Lodgepole Pine (*P. contorta* var. *latifolia*). Exact documentation of these observations has not been possible because the original reports have not been available to us. Mirov only states: "Seed viability may be preserved within the cone for an amazingly long time." After making his tests and finding viability up to five years he said: "There are records of much longer viability of pine seeds, but it is difficult to say how reliable they are."

Our experience with two limbs from the Irish trees was as follows: In limb #1 (Fig. 5), the cone ages ranged from one to twenty-six years. We found fertile seeds up to and including twenty-one years of age, but no germination in years twenty-two through twenty-six. In limb #2 we tested twenty-one cones ranging in age from one to twenty-six years. The twenty-six-year-old seeds did not germinate. Also infertile, however, were seeds from the years two, three and five. Otherwise, all years up to twenty-four showed fertility. In sum, these two experiments showed that seeds can be viable at least up to twenty-four years. Our observation of infertility in seeds older than twenty-four years is of interest. It is clear, however that the limited scope of the experiment prevents general conclusions about maximum age of fertility with respect to the species as a whole.

We were curious about the possible cause of infertility in the cones of limb #2. On external examination and sectioning of the seeds, the twenty-six-year-old specimens all appeared sound but yet did not germinate. In the young infertile years the cones looked sound

* Names in parentheses inserted by present authors.

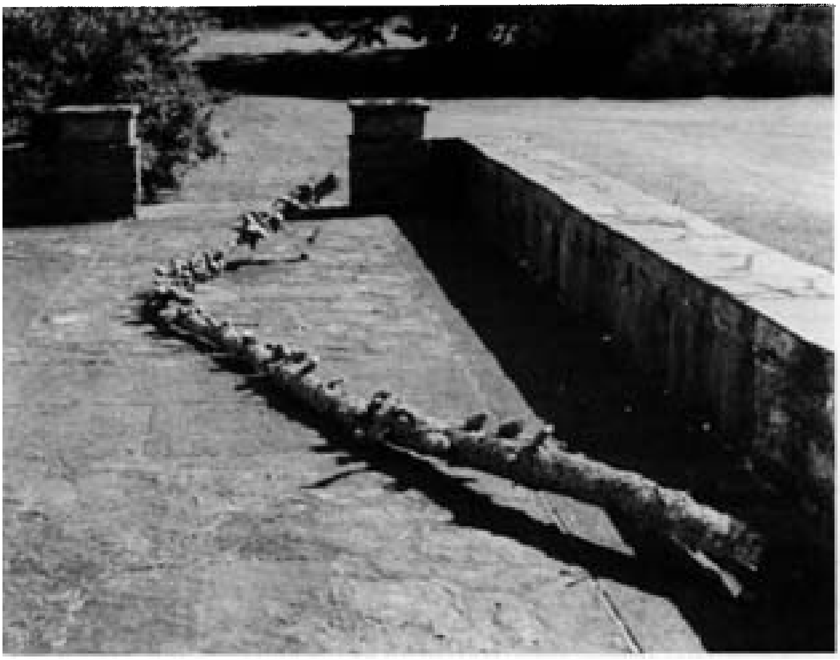

Fig. 5. Limb #1 showing cone whorls spanning twenty-six years. Photo: R. Warren.

but many of the seeds were shriveled or empty. This implies that the older seeds became infertile from aging whereas the younger ones had undergone some injury.

The effect of cone age on the percentage of seeds germinating from a batch of *Pinus radiata* and *P. attenuata* was documented by Badran who found a gradual decrease with time in the production of seeds that germinated. He observed also that the total number of seeds per cone, although varying between specimens, was not related to age. The percentage of empty seeds increased only slightly with age, but not in proportion to the decrease in germination. Thus, age adversely affected many apparently full seeds; furthermore, the time needed for germination was increased in the older seeds. Vogl observed no change in the above features with the passing of time, but the report does not give exact ages.

The number of seeds sown was carefully counted in one of our *Pinus radiata* limbs. We observed great variation in germinating capacities, but, as Badran noted, germination appeared to decrease with age until the last two years (twenty-two and twenty-four) when only one and three seeds, respectively, out of thirty germinated.

One further question that logically arises is whether the cones are living or dead. Although this has not been studied extensively, it is assumed that those that remain sessile must be dead, since the pedicels have become so stretched within the wood. Sargent, already mentioned, found that seeds from cones on a branch of *Pinus contorta*, taken from a tree four and one-half years before, germinated well. We have germinated seeds taken from a tree that had been dead for at least five years. Furthermore, Mirov states: "In the author's experience a *P. attenuata* cone kept at room temperature for twenty-seven years yielded germinable seed." There is not reason to suppose that seeds in a cone on or off the branch should deteriorate if kept at appropriate conditions of temperature and humidity.

Estimation of a cone's age is not always simple. This is particularly so in *Pinus radiata* where additional flushes of growth each year may produce more than one cluster of cones. Counting the number of whorls can thus result in an overestimate. This feature renders slightly unreliable many written reports involving age of cones, since the method of dating, though not usually stated, is assumed to be such a count. The annual growth rings are a reliable method, provided one recognizes that certain dry years may cause rings to be incomplete. Thus, the procuring of a total cross-sectional specimen, rather than a core sampling, is the safest method. The worry about false rings (those caused by a resumption of growth in a year when growth was temporarily arrested by some unfavorable environmental condition) can be allayed by the rarity of this occurrence and the different appearance of false rings from true ones. They fade gradually, both to the outside and the inside, whereas the true ring shows a sharp cutoff externally.

Another method of determining age, according to Badran, is the bunching together of the bud scales and the horizontal constrictions at the nodal points where the terminal buds were forced into a resting period. This is useful for only the first few years of growth, since these landmarks tend to fade with age.

In dating the cones on our two branches we used tree rings, where possible, from cross sections of the limbs. Where this was not possible because of unavailability of the sections, we counted whorls. Where there was a discrepancy between the numbers derived from the two counts, we chose the lesser in order to err on that side rather than to overestimate age.

We made other incidental observations. Although stratification of seeds in cold is not considered necessary for optimum production in *Pinus radiata*, we found in comparing one set stratified for three weeks at 4°C and one not, that the former germinated in 50 per cent to 75 per cent of the interval of time needed for the latter. Cold, however, did not produce fertility in the infertile years.

The farmers in Ireland who grow their own *Pinus radiata* trees open the cones by exposure to direct flame. Early foresters used this method. We tried opening cones by direct flame in a broiler for four to twenty-four minutes, by boiling for two to five minutes, and by heating in an oven (kiln) at 50°C (120°F) for twenty-four to forty-eight hours. Although seeds procured by each method germinated, the kiln method seemed to us the most satisfactory because with it there is no worry about seed damage if heating is carried on too long. We learned that if either of the other two methods is used, the duration of heating should be less than that tried in our experiments; not more than ten to fifteen seconds in boiling water or two to three minutes close to a flame. This is because the cone scales separate gradually after the resin is dissolved. Vogl states that in *P. attenuata*, shedding of seed does not start until one to twelve hours after heating, and that it continues up to three days later. Our impression was that this applies to *P. radiata* also. In using either rapid method for opening cones, it is important that they be removed from the heat after opening has only partially begun. Although it was of interest that boiling for five minutes and direct flame exposure to a 5-inch distance for ten minutes did not hinder germinative ability nor germinative capacity (which occurred in up to 90 per cent of the seeds so procured) there must be a limit of time after which these temperatures will kill seeds.

Badran observed a falling off in the germinative capacity of seeds with progressing years and commented on the apparent soundness ("fullness") of many of the infertile seeds. We found this also; all twenty-nine seeds that did not germinate from the twenty-two year-old cone from limb #2 looked quite healthy externally.

Although arithmetical precision cannot be hoped for in describing these features of the various serotinous species, this does not diminish our sense of wonder at the extreme patience with which these trees wait to protect and reproduce their kind in the face of their natural enemy, fire.

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A Pinus radiata *laden with unopened cones. Photo: M. P. Bollman, New Zealand Forestry Service.*

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