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# Effects of Self-Pollination in the Genus Pinus

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December 9, 1980

## Introduction

The problems of self-pollination among trees are a major concern to foresters. Silvicultural practices have an effect on the frequency of self-pollination. For example, a cut, such as a shelterwood or seed tree, reduces the number of individuals in the breeding population and increases the distance between individual trees. This tends to increase the frequency of self-pollination. These effects can either be helpful or harmful depending on the goals of the forester. Therefore, a basic understanding as to the effects of self-pollination on trees is necessary. The point of focus in this paper is the genus, Pinus.

Self-pollination occurs naturally in the forests, but usually not to any great extent. Trees have phenological and morphological barriers to self-pollination that help reduce the frequency. When self-pollination does occur, recessive genes that may be carried in the heterozygous condition can be expressed. These can either cause various degrees of harmful changes or go unnoticed. Because only the lethal or deviant changes are highly observable, those are the ones associated with self-pollination. Therefore, self-pollination is generally thought of as being harmful.

Self-pollination can also carry out an important function in the forest. When the environment changes, trees need to cope with that change. The variation carried in the genes of the population allow the species

to adapt to environmental changes. A recessive gene that
was once considered harmful can be necessary for the sur-
vival of the species. Self-pollination does have its
place, but in the normal forest situation, outcrossing
is the more common method of pollination.

## Review of Literature

The effects of self-pollination of pines have been
documented for years. In 1945, Johnson showed that selfing
had no appreciable effect on seed set for eastern white
pine (Pinus strobus), but for P. sylvestris and P. resinosa
a marked reduction in seed set occurred. He also reported
that one-fourth of the selfed seedlings of both Scotch pine
(P. sylvestris) and white pine were smaller in mean spread
and height and lower in mean weight than the crossed
seedlings.

Mergen (1954) showed that selfed slash pine (P.
elliottii) seedlings exhibited less height growth in com-
parison to the crossed seedlings. Bingham and Squillace
(1955) reported height depression in 16 of 19 western
white pine (P. monticola) seedlings. They stated that
selfing did not affect cone yield, but it did decrease
mean sound seed yield per cone by 50 per cent. Hollow
seed yields from selfing were 275 per cent above crossed
yields.

Working with Scotch pine, Ehrenberg et. al. (1955)
reported that pine self-fertilization leads to an increase
in seed abortion. Although there was no completely
self-incompatible tree, seed set still decreased and
empty seed yields increased with self-pollination. A
higher degree of polyembryony also occurred.

Squillace and Bingham (1958) promoted the idea of
"selective fertilization" to account for the greater

success of cross-pollen over self-pollen in mixed pollen studies. The different self-incompatibilities of trees could be explained by the different degree of selective fertilization, also.

In a following study, Barnes, Bingham, and Squillace (1962) reported that sound seed yields were consistently lower than cross yields in partially self-fertile western white pines. However, selfed yields were nearly equal or greater than cross yields from completely self-fertile trees. Inbreeding depression was observed in the progeny from partially self-fertile trees.

Squillace and Kraus (1963) studied the types of albino mutants produced by selfed slash pines. They also noted a tendency for the chlorophyll deficiencies produced by selfing to follow a geographic pattern, but they offered no definite conclusions. In another paper (Kraus and Squillace 1964) they stated that the degree of natural selfing among slash pines was approximately 7 per cent. They proposed that the decreased yields observed after selfing were probably the result of post-fertilization competition rather than pre-fertilization competition among embryos.

Barnes (1964) noted that western white pine selfed seedlings were slower growing and had poorer survival rates than crossed seedlings. The rates of inbreeding depression varies from 15 per cent for completely self-fertile trees to 40 per cent for partially self-fertile trees.

Fowler (1965a and 1965b) found that selfed red pine seedlings exhibit little or no inbreeding depression. He did find some harmful effects among jack pine (P. banksiana) and eastern white pine selfed seedlings. Although jack pine showed no significant difference for number of cones set, number of seeds per cone, or per cent germination; the selfed seedlings had shorter hypocotyls, higher mortality at 6 weeks, and more cotyledons per embryo. Eastern white pine also showed no significant difference for per cent germination, per cent of full seed, and per cent of full seeds per cone; but twisted needles occurred in 15 per cent of the selfed seedlings and a lack of apical dominance in 12 per cent. Two deviant types, on chlorotic and the other slow-growing, were observed. Fowler (1965c) stated that selfed progeny of jack pines were "clearly inferior" to those of crossed trees.

Snyder and Squillace (1966) studied slash, longleaf, loblolly, and shortleaf pines and found that selfed seedlings produce only one-eighth to one-sixth as many seeds per cone as crossed seedlings. Snyder (1968) reported a 24 per cent decrease in height for moderately self-compatible slash pines over the crossed seedlings.

Franklin (1969) observed the different mutants of loblolly (P. taeda) pine seedlings. He found chlorophyll deficiencies primarily, but also stunting and dwarfing occurred. In 1970, Franklin authored a paper on the mutant forms of the Pinaceae (Pine family). He described

these forms for 11 species of pine and reported yield
and growth differences for 16 species.

After studying ponderosa pine (P. ponderosa)
seedlings, Sorenson (1970) found no significant difference
in the development of conelets, number of sound seeds, or
per cent germination. However, the yield of filled seed
decreased from 66.5 filled seed per 100 round seed from
crossings to 23.7 filled per 100 round from selfings.
Selfed seeds were also slightly smaller in size and
their first-year survival was significantly less.

Bramlett and Porham (1971) derived a model for
determining the number of unsound seed produced from
selfing. Franklin (1971) estimated the degree of natural
selfing of pines based on the mutant forms produced.

Sorenson and Miles (1974) found that seed set from
ponderosa pine selfings was about 35 per cent that of
crossings. They observed no difference in seed weight,
but the germination percentage for selfed seeds was less.
Height depression for selfed seedlings was 21 per cent
the first year and increased in the following year.

# Discussion

## Pinus sylvestris (Scotch Pine)

Although no self-incompatibility seems to exist in Scotch pine (Ehrenberg, et. al. 1955), it still exhibits reduced vigor and reduced growth when self-pollinated (Johnson 1945). Reductions in seed set, the amount of filled seed, average height, and average weight occur. The selfed seedlings have a reduced capacity to survive and a slower growth rate when compared to open-pollinated seedlings (Ehrenberg, et. al. 1955; Johnson 1945). The data are summarized in Tables I and II.

Ehrenberg, et. al. (1955) notice a higher degree of polyembryony among selfed seedlings, but offer no explanation. One possibility is that the genotypes of selfed embryos are so similar that one does not have a clear competitive advantage over others. Therefore, several embryos develop for a longer period of time than with crossing.

Table I. Seed set and seedling emergence from controlled selfing, controlled crossing, and open pollination of Scotch pine conelets (from Johnson 1945).

| source | number of bags | number cones collected | number seeds | seed set% | number emerged | emer-gence |
|--------|---------------|------------------------|--------------|-----------|----------------|------------|
| S1 open | -- | 5 | 76 | 60 | 36 | 47 |
| S1 x S2 | 3 | 1 | 18 | 72 | 8 | 44 |
| S1 x S1 | 4 | 5 | 40 | 31 | 4 | 10 |

Mutant forms of Scotch pine occur under open-pollinated conditions, and these mutants usually exhibit some chlorophyll deficiencies (Franklin 1970). Under open conditions, it is difficult to determine whether these mutants result from self-pollinated or cross-pollinated seeds.

Table II. Mean values for certain quantitative characters of 4-year old Scotch pine seedlings (from Johnson 1945).

| source | mean number seedlings | mean spread (inches) | mean height (inches) | mean weight (grams) |
|---|---|---|---|---|
| S1 open | 10 | 19.5 | 22.1 | 624 |
| S1xS2 | 8 | 23.4 | 23.6 | 609 |
| S1xS1 | 4 | 14.9 | 14.8 | 323 |

## Pinus elliottii (Slash Pine)

Slash pine appears to be much less self-compatible than other pine species. Kraus and Squillace (1964) estimate that the degree of natural selfing is only 7 per cent. Seedling yield per cone decreases greatly after selfing, and even highly self-compatible trees have unusually high mortality rates during germination (Kraus and Squillace 1964; Snyder 1968). (See Table III.) Albino frequencies vary from 0.4 to 7.6 per cent for wind-pollinated seedlings and are 32.4 per cent for selfed seedlings (Squillace and Kraus 1963).

The reasons for the low self-compatibility of slash pine are not known. Some factors under consideration are low seed germination, production of fewer sound seed

per cone, and high embryo mortality due to homozygous
recessive lethal genes (Kraus and Squillace 1964). These
factors are involved with every selfed species, so some
other factor must be contributing to the relatively low
self-compatibility.

Kraus and Squillace (1964) suggest that the high
degree of selective fertilization that occurs is one of
the controlling factors in low self-compatiblity. When
equal mixes of self- and cross-pollen are applied to a
cone, the cross-pollen produces more sound seed. If the
different pollens are equally capable of fertilization,
then a 50:50 ratio of seed production should occur.
However, it does not. The cross-pollen is more efficient
in fertilizing the egg. The exact reasons for this are
not known and would be difficult to ascertain.

Although Kraus and Squillace (1964) suggest that
selective fertilization is the primary reason for the
low self-compatibility in slash pine, selective fertiliza-
tion occurs in all species of pine. The relatively low
degree of self-compatibility cannot be related to only
selective fertilization. The unknown factors which
regulate selective fertilization may exert more control
and decrease self-pollination. Life history events, such
as the phenology of reproduction or the difference in
release time of pollen and receptivity of the megasporan-
gia, could also affect self-pollination, but these events
have not been evaluated for slash pine.

Another interesting fact about slash pine is the
occurrence rate of albino mutants. The albinos, charac-

terized by reddish to reddish purple hypocotyls and
white or pale yellow cotyledons, die within two weeks
after germination (Squillace and Kraus 1963). Squillace
and Kraus (1963) calculate that these albinos occur at a
frequency of 0.052 (1 in 2000) in the population. Since
the mutant is lethal, this indicates that the mutation
rate is about 0.052, much higher than the average 1 in
100,000 rate. If the mutation rate is not that high,
then another factor must be involved. Squillace and Kraus
(1963) suggest that natural selection is favoring the
heterozygotes over both of the homozygotes. That is,
the lethal gene remains in the population for a longer
period of time than would normally occur. Usually, a
lethal gene is removed from the population as it becomes
expressed. Although the idea of Squillace and Kraus (1963)
is interesting, it has not been verified.

Table III. Seed yield and germination in self- vs.
cross-pollinations and relative yield of self-pollinated
seedlings (from Kraus and Squillace 1964).

| tree no. | seed yield/cone self vs. cross | | seed germination self vs. cross | | seedling yield/cone self vs. cross | |
|---|---|---|---|---|---|---|
| 1 | 7 | 7 | 6 | 39 | 0.4 | 6.6 |
| 10 | 29 | 45 | 22 | 56 | 6.4 | 25.2 |
| 11 | 3 | 5 | 3 | 55 | 0.4 | 2.8 |
| 27 | 42 | 23 | 7 | 44 | 2.9 | 40.1 |
| 29 | 3 | 52 | 54 | 76 | 4.6 | 39.5 |
| 193 | 10 | 15 | 42 | 78 | 4.2 | 44.7 |
| 194 | 12 | 46 | 70 | 68 | 8.4 | 40.5 |
| aver. | 15.1 | 27.6 | 29.1 | 62.3 | 3.9 | 28.5 |

Pinus taeda (Loblolly Pine), P. echinata (Shortleaf Pine),
   P. palustris (longleaf Pine)

Snyder and Squillace (1966) report that the survival
of selfed cones is not significantly varied from that of
cross- and wind-pollinated cones for P. taeda, P. echinata,
and P. palustris. However, the number of seeds per selfed
cone is only one-eighth to one-sixth that of cross- and
wind-pollinated cones.

The problem with the data is that the results are
probably biased. The authors state several reasons for
this including poor counting techniques, lack of considera-
tion for insect problems, and weather effects. The data
probably do not reflect the actual relationship among the
pollination types. However, since the decrease in the
number of seeds per cone is so large, it can be assumed
that some reduction does occur after selfing, even if
the actual percentage is smaller.

Several mutant forms of loblolly pine have been
observed by Franklin (1969). Most of them involve
either some type of chlorophyll deficiency or stunting.
Twenty-two different mutant forms were observed in 30
(25 per cent) of the 119 loblolly groups observed.

Pinus ponderosa (Ponderosa Pine)

Ponderosa pine is highly varied in its degree of
self-compatibility among trees. One study has values
ranging from 4 per cent to 76 per cent (Sorenson 1970).
In connection with this is the per cent of filled seed

from different types of pollination. (See Table IV.)
These values are also highly variable, but when averaged,
the selfed values are significantly lower than those for
cross- and open-pollinated cones.

Table IV. Number of filled seed per 100 round seed for
self-, cross- and open-pollinated cones (adapted from
Sorenson 1970).

| pollination type | range of filled seed high | low | average number of filled seeds |
|---|---|---|---|
| self | 47.6 | 2.0 | 20.7 |
| cross | 89.7 | 41.5 | 66.5 |
| open | 87.1 | 41.5 | 75.2 |

Selfing of ponderosa pine produces other effects on
seeds. Selfed seeds have a higher proportion of undersized
or weakly developed embryos than seeds from cross- and
open-pollination (Sorenson 1970; Sorenson and Miles 1974).
Due to this, germination percentages are lower for selfed
seeds. If only seeds with full-sized embryos are consid-
ered, there is no significant difference among the percent-
ages for the different types of pollination (Sorenson 1970;
Sorenson and Miles 1974).

Selfed seedlings have the lowest first-year survival
rate of the three types of pollination. This is not due
to some overall weakness in the seedlings, but to the
appearance of homozygous recessive lethal genes in the
seedlings. If these seedlings (ones with lethal genes)
are eliminated from the survival percentages, then there
is no significant difference among the rates (Sorenson
1970). However, the fact that these recessive genes

do occur is an important effect of selfing that cannot be overlooked.

Height depression of first-year seedlings averages 21 per cent and increases with age (Sorenson and Miles 1974). This indicates that the growth rate of the selfed seedlings is generally slower than that for crossed seedlings. Inbreeding depression is not just a one-year occurrence; it continues throughout the life of the selfed progeny.

## Pinus monticola (Western White Pine)

Like most other pine species, western white pine shows a variety of responses to selfing. Generally, cone yield is not significantly affected; sound seed yield per cone decreases by 50 per cent in some instances; germination reduces by 10 per cent; height growth depression ranges from 15 to 40 per cent for first-year selfed seedlings, 13 to 30 per cent for second-year seedlings, and 10-25 per cent for third-year seedlings (Barnes 1964; Bingham and Squillace 1955). The selfed seedlings are usually slower growing, and mean epicotyl lengths are shorted (Squillace and Bingham 1958; Barnes 1964; Barnes, Bingham, and Squillace 1962). Numbers of cotyledons and mean sound seed weight are not significantly affected (Squillace and Bingham 1958).

When observing the sound seed yield per cone data, it becomes apparent that selfing does not always decrease yields (see Table V ). Those trees which are termed

self-fertile do not exhibit the deleterious effects of selfing suffered by most trees. In studies (Squillace and Bingham 1958; Barnes et. al. 1962), it is considered as a result of differences in the degree of selective fertilization. The self-pollen from these trees is not discriminated against as heavily as it is in other trees. It is able to compete with other pollens in the "race" to fertilize the egg. The genetic variation among trees responsible for this is not understood.

In partially self-fertile trees, the mixture of self- and cross-pollens produce seeds that are closer to cross-pollen seeds in measurements (Squillace and Bingham

Table V. Sound seed yield after outcrossing and selfing (from Barnes et. al. 1962).

| seed parent | crosses | outcrossing sound seed/ cone | selfing sound seed/ cone |
|---|---|---|---|
| 58 | 11 | 106 | 134 |
| | 2 | 78 | 89 |
| | 3 | 104 | 104 |
| | average | 96 | 109 |
| 69 | 3 | 84 | 87 |
| | 2 | 120 | 118 |
| | average | 102 | 102 |
| 54 | 4 | 106 | 80 |
| | 3 | 110 | 102 |
| | 2 | 157 | 110 |
| | average | 124 | 97 |
| 64 | 4 | 56 | 6 |
| | 3 | 182 | 71 |
| | average | 119 | 39 |

1958; Barnes et. al. 1962).  Most of the western white
pines tested fit into this category.  Presumably, the
cross-pollens are more effective in pollinating the eggs,
even though the tree has some degree of self-compatibility.

In order to explain the relative efficiencies of
different pollens in competition for fertilization,
Barnes et. al. (1962) note that a positive correlation
exists between parent tree growth rate and pollen tube
vigor.  However, this does not mean that pollen from a
fast-growing tree will be the most effective in fertiliza-
tion.  Pollen from a slow-growing tree, due to the out-
comes of meiosis, may be able to outcompete pollen from
a fast-growing tree.

## Pinus strobus (Eastern White Pine)

Selfing of eastern white pine can produce a chloro-
phyll deficient mutant at the frequency of 25 per cent
(Johnson 1945).  The mutant is white to cream-colored
and shortly dies.  Although selfing does not affect seed
set, the number of filled seeds per cone, the number of
filled seeds, or the per cent of germination; a reduction
in vigor, height, and weight of seedlings has been
observed (Johnson 1945; Fowler 1965b).  (See Table VI.)

## Pinus resinosa (Red Pine)

According to Fowler (1965a and 1965b), red pine is
different from most other pine species studied because
it does not exhibit a great deal of inbreeding depression.

He states that red pine is extremely uniform both morpho-
logically and genetically, yet it is capable of surviving
and reproducing over a wide range of climatic conditions.
Part of this homogeneity is due to its inhabiting areas
after fires. Unlike serotinous species, red pine must
rely on the remaining population for its seed source.
Since the population has decreased due to the fire, the
variation has decreased also. Fowler claims that succes-
sive generations of such reproduction have resulted in
the rapid elimination of deleterious mutant genes. It
has also had the tendency to maintain the homozygosity
of the species. Since the species is composed of mostly
homozygous alleles, selfing would not have the effects
on it observed in other pine species. Fowler (1965a)
notes that little inbreeding depression occurs and only
1 out of 46 seedlings was aberrant. If his hypothesis
is valid, then it could be applied to other nonserotinous
species which reforest areas after disturbances. No
record of such further investigation is found in the
Pinus literature.

Table VI. Mean values for certain quantitative
characters of 4-year old white pine seedlings (from
Johnson 1945).

| source | number seedlings | mean spread (inches) | mean height (inches) | mean weight (grams) |
|---|---|---|---|---|
| W1 open | 27 | 7.7 | 8.5 | 121 |
| W1 x W2 | 27 | 7.0 | 7.9 | 114 |
| W1 x W1 total | 46 | 5.0 | 6.2 | 64 |
| W1 x W1 green | 35 | 5.0 | 6.6 | 75 |
| W1 x W1 albino | 11 | 4.0 | 4.7 | 50 |

Although continual inbreeding has probably reduced the heterozygosity of red pine, a better explanation for low heterozygosity and relatively high self-compatibility has been supported in recent years. During the last stages of Wisconsin glaciation, red pine, along with other tree species, was forced from its normal range (see Figure I). The population of red pine was reduced to a few isolated refuges in the eastern Appalachians (Cook, Smith, and Stone 1952). This drastically reduced the population, forcing it through an "evolution bottleneck" (Fowler and Morris 1977). Such a drastic reduction in population size decreases the average and overall heterozygosity of the species (Nei, Maruyama, and Chakraborty 1975). Only a small proportion of the original heterozygosity of the species remains in the refuge population.

If the only method of increasing variation is by mutation, then it will take millions of years for a tree population to recover its variability (Nei, Maruyama, and Chakraborty 1975; Fowler and Morris 1977) due to the slow mutation rate. Red pine completed its migration into its present range about 8000 to 11000 years ago (Cook, Smith, and Stone 1952; Fowler and Morris 1977). Therefore, time has been too short for the species to recover its hetero-zygosity, and it has remained relatively homozygous in comparison to other pine species.

Red pine is not entirely homozygous, and some lethal recessive genes cause mutant selfed seedlings (Fowler 1965a). One of these is a form of albinism in which the cotyledons are light yellow-green and the hypocotyls pink (Franklin

1970). The frequency of this mutant suggests that it is the result of a single locus with two alleles.

## Pinus banksiana (Jack Pine)

Although jack pine occurs in the same general area as red pine and also germinates after fires, it is much more heterozygous (Fowler 1965b). This is due in part to the serotiny of the cones. These cones maintain elements of the gene pool that would otherwise be lost. When a fire occurs, trees are removed from the breeding population. If these trees have produced serotinous cones which will produce new trees, then part of their genetic variation has been retained in the population.

As a consequence, selfing of jack pine results in inferior progeny (Fowler 1965c). The proportion of filled seed drops from 60.2 per cent after cross-pollination to 11.0 per cent after selfing (Fowler 1965b). Of the 15 cases of reverse germination (see Appendix B) observed, 11 of those were the result of self-pollinations (Fowler 1965b).

Seedlings from selfings have shorter hypocotyls, a higher mortality rate, and a greater number of cotyledons than those from cross-pollination. Chlorotic and dwarfed seedlings have also resulted from selfings in some instances.(Fowler 1965b).

0    100   200
MILES

●   present refuge
    populations

- - - - ⌐ edge of wisconsin
           glaciation

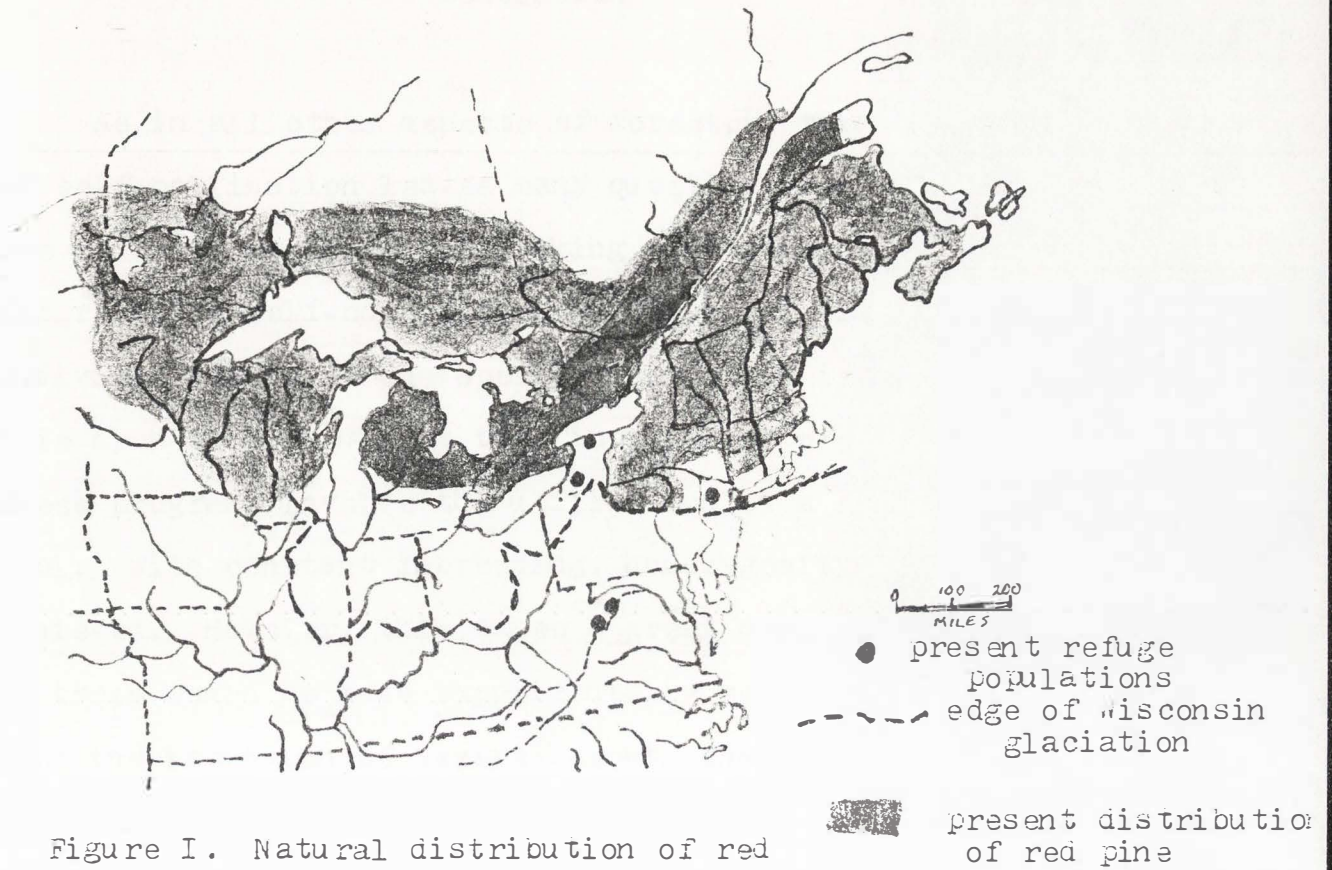        present distributio:
        of red pine

Figure I.  Natural distribution of red
pine on the North American continent, with
the southern-most limits of wisconsin glaciation
superimposed (from Cook, Smith, and Stone 1952).

# Conclusion

As in all other aspects of forestry, the subject
of self-pollination leaves many questions unanswered.
One of the most thought-provoking questions deals with
the relative self-compatibilities among species and among
individual trees of one species. Research is needed in
this area to aid current tree improvement programs.
These programs involve the utilization of a small gene
pool. With constant inbreeding, homozygosity can be
achieved. However, this takes a great deal of time.
If trees could be made experimentally more self-compatible,
then the isolation of desired growth characteristics or
resistant genotypes could be facilitated.

The details of self-compatibility are still virtually
unknown. Why a strobilus is more receptive to some types
of pollen than others is still unanswered. The question
of embryo competition has only recently been investigated
thoroughly, but no definite conclusions have been reached.
If the effects of self-pollination and their impact on
forest dynamics are to be understood, then more research
is needed in the microscopic details of fertilization.

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Descriptions of abnormal phenotypes for various pines
species (adapted from Franklin 1970).

Pinus banksiana          small, chlorotic, short cotyledons
                             (usually 4); lethal at 3 to 4
                             weeks
                         pale-yellow cotyledons, developing
                             normal pigments at about 6 weeks
                         white cotyledons, developing normal
                             pigment at about 6 weeks
                         inverted germination--cotyledons appear
                             first
                         cotyledons normal-green; primary
                             foliage yellow
                         thick, twisted, light-green hypo-
                             cotyl; twisted, thick cotyledons
                         bright yellow-green hypocotyl
                         primary foliage short, thick,
                             bluish-green; epicotyl dwarf

P. elliottii             yellow oleoresin
                         virescent; yellow-green foliage
                             turning green toward end of
                             first season
                         albino (lethal)
                         xantha-yellow cotyledons (lethal)
                         xantha-yellow-green cotyledons

| P. elliottii | viridis light-green cotyledons |
| --- | --- |
| P. jeffreyi | albino (lethal) |
| P. monticola | albino (lethal) |
| P. radiata | dwarfs with short, distorted needles |
| | needles partly fused within a fascicle |
| | bright-green, fused cotyledons (lethal) |
| | albino (lethal), some yellow or pale green pigments noted |
| | repeated dichotomies in the shoots, seen at 2 years and older |
| | tips of cotyledons blood-red as seed-coat is shed |
| | seedling primary needles golden in color |
| | bluish foliage; shortened, recurved primary leaves; stunted |
| | golden-yellow cotyledons and primary needles (lethal) |
| | pale, almost white cotyledons; green primary needles |
| | green cotyledons; pale, almost white primary needles |
| P. resinosa | light yellow-green cotyledons and pink hypocotyls (lethal) |
| | chlorotic at germination, becoming normal at about 1 month |

P. strobus        emerging needles white to cream,
                      changing through the season to
                      yellowish-white or yellowish-green,
                      and light green in fall
                  predisposition to forking due to
                      lack of apical dominance
                  twisted needles from the same trees
                      as above


P. sylvestris     emerging needles yellowish-white
                      changing to light green in late
                      season
                  albino (lethal)
                  yellow cotyledons (lethal)
                  greenish-yellow cotyledons
                  light green to yellowish-green
                      cotyledons
                  primary foliage white and short;
                      secondary foliage not produced
                  primary foliage yellow and short;
                      secondary foliage yellow if
                      produced
                  primary foliage whitish-green or
                      green in the first pairs; secondary
                      foliage contains white and shades
                      of green and yellow
                  primary foliage green, grading to
                      yellow in upper epicotyl; secondary

P. sylvestris          foliage yellow

( cont.)          primary and secondary foliage

light green in varying shades

Selected definitions*

Albinism:  Complete or almost complete absence of usual
        color caused by lack of pigment and resulting in
        white color.

Biotype:  An individual or group of individuals of the
        same genotype with respect to one or more characters.

**Cotyledons:  One or more leaflike appendages
        present in the embryo.

Cross-pollination:  Pollination of a biotype
        with pollen from one or more different
        biotypes.

Dominance:  The relative effectiveness of an
        allele in masking the action of a different allele
        with which it is paired.

**Epicotyl:  The shoot part of the embryo or seedling above
        the cotyledons consisting of an axis and leaf primordia.

***Evolution bottleneck:  A drastic reduction in population
        size of a species which results in a reduction in the
        heterozygosity of the species.  It is usually the
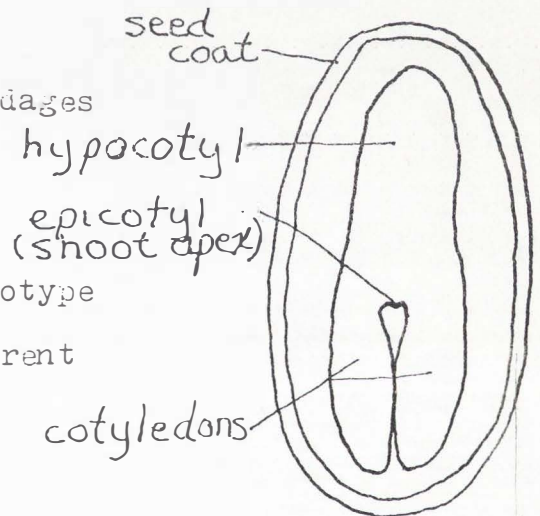        result of some environmental factor forcing the



Figure 1. Embryo

seed coat
hypocotyl
epicotyl (shoot apex)
cotyledons

population to exist in a "refuge" situation.

Fertilization: The union of the nucleus and other cellular
constituents of a male gamete (sperm) with those of
a female gamete (egg) to form a zygote from which a
new plant develops.

@Filled seed: Seed in which a viable embryo exists.

Genotype: (1) An individual's herediatry constitution,
expressed or hidden, underlying one or more characters.
(2) Individual(s) characterized by a certain genic
constitution.

Heterozygosity: Presence in an organism of different
members of the same allelic set.

Homozygosity: Presence of identical alleles, either both
dominant or both recessive.

**Hypocotyl: Axial part of embryo or seedling located
between the cotyledon or cotyledons and the
radicle.

@Inbreeding depression: A decrease in height, width,
or some other characteristic due to selfing
in comparison to cross-pollinated seedlings.

Incompatibility: A failure or partial failure in
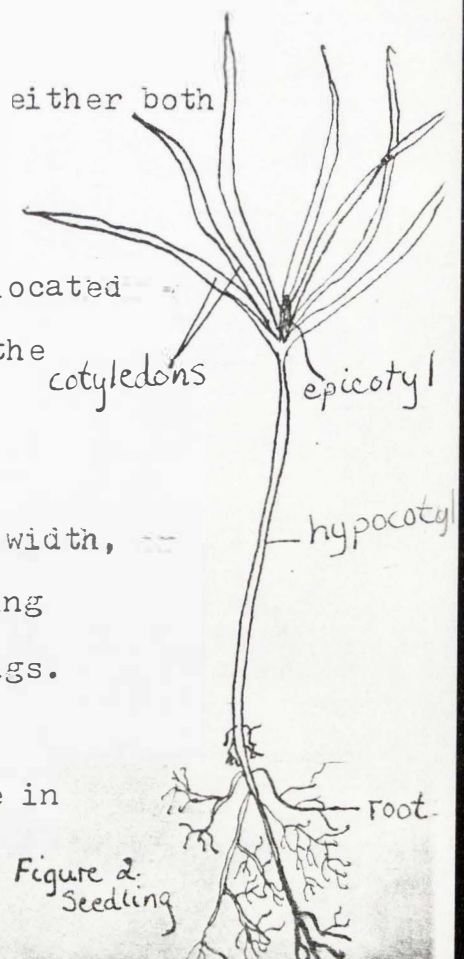
cotyledons    epicotyl

hypocotyl

foot

Figure 2.
Seedling

some process leading to fertilization even though the egg and sperm cells are potentially functional.

Meiosis:  Specialized nuclear divisions prior to the formation of gametes (either eggs or sperm).  Usually the first meiotic division reduces the chromosome number by one-half (2N to N) because, after pairing, one chromosome of each pair moves to each daughter cell.  In the second division, each chromosome of the newly formed haploid (N) daughter nuclei divides so that the end result of meiosis is four cells, each with half the original number of chromosomes.

Mutation:  A sudden variation from the ancestral phenotype, due to gene or chromosome changes.

Open-pollination:  Pollination effected by wind, insects, etc., and not directly influenced by man.

Phenotype:  (1)  The demonstrable characteristic(s) of an organism; the product of the interaction of the genes of an organism with the environment.  (2)  Individual(s) described on the basis of demonstrable characteristics.

Pollination:  The transfer or pollen to the receptive part of the female flower.

**Polyembryony:** Development of more than one embryo in a single seed.

Recessiveness: Converse of dominance.

@Reverse germination: Embryo is reversed in relation to the micropyle; cotyledon-bearing tip emerges from the micropylar end, while the radicle remains enclosed in gametophyte tissue.

@Round seed: Seed that has the typical shape for the species.

@Selective fertilization: The process by which the egg can control which pollen is able to fertilize it, presumably due to chemical inhibitions. Can also refer to pollen competition.

Self-incompatibility: Genetically controlled physiological hindrance to self-fruitfulness.

@Sound seed: Seeds that contain fully-developed embryos.

*Unless otherwise indicated, definitions from Snyder,E.B (ed.). 1959. Glossary for forest tree improvement workers, SAF.; and Allard, R.W. 1960. Principles of plant breeding, Wiley, N.Y.

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