WHITE PINE POLLEN SPECIES AND YEAR DO NOT AFFECT CONELET DROP OR CONE SIZE IN *PINUS STROBUS*

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ABSTRACT--Statistical analysis of 6 years' breeding experiments on *Pinus strobus* L. showed that conelet drop was controlled by female parent but not by white pine pollen species or year of pollination. Crossing with a species never yielding viable seed did not increase conelet drop. The degree of loss was the same after self- and open-pollination as it was after controlled crossing. The length and weight of mature cones also depended only on female parent. A possible relation is suggested in pines between the presence or absence of a pollen effect on cone retention and the type of crossability barrier.

Premature cone drop in pines is a widespread and serious problem in many species. It is especially frequent in the first part of the conelet stage, i.e., early in the first year of cone development.

Abscission of conelets during the first few weeks after pollination may result from severe competition with vigorously growing vegetative shoots for photosynthates and mineral nutrients (Sweet and Bollman 1970). It also appears to be associated with a threshold proportion of aborted ovules per cone (Burdon and Low 1973b).

In regions where pollen supply is limited, wind pollination may be insufficient for cone retention. If most of the ovules are not pollinated, they collapse in a few days and the conelet drops off (Sarvas 1962).

Cone losses due to wind, animals, birds, and insects may occur at any time during cone development but are most common at later stages, especially during the second year.

The degree of maternal control over conelet drop varies among individuals. Clonal tests of *Pinus sylvestris* L. have shown that trees vary widely in the amount of pollen required to retain conelets (Brown 1970). Clonal variation in conelet drop in *Pinus radiata* D. Don, where pollen supply is not a problem,

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may be due to clonal differences in spring growth patterns because of the critical competition with vegetative growth (Sweet and Bollman 1970).

The pollen parent had no effect on conelet drop in intraspecific crosses of Pinus resinosa Ait. (Fowler 1965b). In Hagman's crosses between species and between subgenera of pines, there was no effect in crosses of Pinus peuce Griseb. and Pinus cembra L. with other white pines, regardless of crossability. A pollen parent effect was apparent, however, in crosses of these pines with hard pines. In P. sylvestris, the male effect varied from nil to high in species crosses within the hard pines and was pronounced in crosses with white pines. [2]

Conelet drop is a serious problem in P. strobus. In Ohio, heavy losses occur during the first 4 weeks after pollination. Records suggest that there were differences in conelet drop among trees used in breeding experiments in Ohio. This led to analysis of crossing records to estimate male and female parental effects as an aid in the selection of breeding materials. The availability of 6 years' data permitted analysis of the possible effect of year of pollination as an indication of nongenetic effects.

METHODS

Crossing Technique

Crosses were made in young stands and plantations of P. strobus in north central Ohio. They included selfs, P. strobus crosses, and crosses with other white pines. Standard pollination procedures were used with adequate precautions for protection from contamination. For each cross combination, records were kept of the pollen parent, number of strobili pollinated, number of corselets bagged for insect protection, and number of cones collected at maturity. Yield of filled and empty seed was recorded. Lengths and weights of cones from 4 years' collections were measured after air-drying and seed extraction.

Analysis

Analysis of conelet drop in interspecific crosses followed the procedure in the generalized least squares program for partial regression developed by Barr and Goodnight (1971). An analysis of variance was run on cone yield data per tree x tree combination for the 6 years 1962, 1963, 1964, 1965, 1966, and 1969 in relation to the number of strobili pollinated. Estimates of the effects of year, male species, and female tree were obtained. Because of the large number of levels involved, the individual male parent effect was excluded from the analysis. This effect, if any existed, would be smaller than the effect of pollen species. If pollen species were nonsignificant, the individual male parent could

[2] Personal communication with M. Hagman.

therefore be assumed to have no significant effect on conelet drop.

Comparisons of the effects of selfing vs. outcrossing and of controlled vs. open pollination on cone yield per flower were made by "t" tests of trees on which both types of cross were made.

Estimates of the effects of year, pollen species, individual pollen parent, and female tree on cone length and cone weight were also obtained from a least squares analysis of variance. The analysis was based on the mean of each tree x tree combination for all crosses made from 1962 through 1965.

The effects of selfing vs. outcrossing and of controlled vs. open-pollination on cone length and weight were compared by "t" tests.

RESULTS

Mean cone yield, cone length, and cone weight are summarized in table 1 by species cross. Analysis by tree combination showed:

1. Conelet drop was strongly controlled by the individual female parent (p of a larger F = 0.0001).

2. Pollen parent had no significant effect on conelet drop even when it was another species of white pine, either crossable or noncrossable in terms of sound seed yield.

3. Neither selfing nor open pollination affected conelet drop in comparison with controlled intraspecific cross-pollination.

4. Year of pollination had no effect on conelet drop when adjusted for male and female parent.

5. There was no effect of pollen species, pollen parent, year, selfing, or open pollination on length or weight of dry mature cones.

DISCUSSION

Biological Relations

The absence of a pollen parent effect on conelet drop in *P. strobus* is typical of at least two other white pines, as previously noted. A negligible pollen parent effect on cone length has also been observed in other pines (Fowler 1965a, Burdon and Low 1973a).

The accumulated evidence from these experiments and others covers a diversity of species and suggests that there is a common factor in the pollen of white pines favoring cone retention, cone scale development, and seed coat formation.

Table 1.--Cone yield, cone length and weight, and sound seed yield of *P. strobus*

Cross combination	Female parents	Strobili pollinated	Mean cone yield 1/	Mean dry cone length	Mean dry cone weight 1/	Mean sound seeds per cone
INTERSPECIFIC CROSSES						
	No.	No.	Percent	cm	gm	No.
P. strobus x						
griffithii	15	1,067	21	10.6	7.9	9.4
monticola	14	3,619	21	9.0	5.4	4.4
peuce	17	2,572	19	8.4	5.4	1.7
peuce x *strobus*	5	334	19	10.4	6.8	.5
parviflora	9	360	18	9.5	5.9	6.8
flexilis	10	1,056	23	9.4	5.8	.0
albicaulis	2	343	05	10.0	5.8	.0
cembra	10	879	15	12.0	7.3	.0
koraiensis	4	274	11	2/	2/	.0
INTRASPECIFIC CROSSES						
P. strobus x						
strobus outcross	41	10,464	19	9.4	6.3	19.3
strobus open	9	438	20	9.6	6.8	19.6
strobus self	17	911	19	9.4	5.9	11.5

1/ Differences nonsignificant at p = 0.05 (see Methods).
2/ No measurements taken.

Diffusible pollen-wall enzymes appear to play a role in pollen-tube nutrition and growth (Stanley and Linskens 1965, Knox and Heslop-Harrison 1970) and might be involved in cone nutrition. Genetic factors in pollen controlling the production of sugars and critical to ovule development may function in the nucellar tissue (Hagman 1975) but in at least some species, e.g., *Pinus thunbergiana* Franco, pollen viability is not a requirement for conelet retention (Katsuta 1971).

White pines seem to have embryo inviability as an isolation mechanism (Hagman and Mikkola 1963, Kriebel 1972). It is possible that a common pollen factor in these pines initially induces cone scale development and later stimulates pollen tube growth and fertilization. Subsequent control is through genome interaction, leading either to full seed formation or embryo abortion, depending on the species combination.

In contrast, incompatibility with arrested pollen tube growth is the typical reproductive barrier in *P. sylvestris* and other hard pines investigated (McWilliam 1959, Vidakovic' and Jurkovic'- Bevilacqua 1970). Hagman found that *P. sylvestris*, unlike the soft pines, has a higher rate of conelet drop in inter- or intra-sectional crosses than in crosses within the species. Clearly, some pollen stimulus to cone retention occurs in *P. sylvestris*, because all the cones in incompatible species crosses do not abort, but the effect on the strobilus is insufficient for full pollen tube growth and fertilization. All hard pines may not have male-induced conelet drop, but it is evident that they do not share a pollen factor favoring cone retention in interspecific crosses.

The finding that conelet drop was no higher in *P. strobus* after selfing than after outcrossing agrees with results of other selfing experiments on both soft and hard pines. Pollen-tube incompatibility has never been observed in either subgenus of pines in response to self-pollination (Hagman 1964, 1975). The reaction to selfing occurs after fertilization. Therefore, the results of selfing *P. strobus* tend to support the suggested relation between post-fertilization ovule abortion and polen-induced cone retention in inviable crosses.

Practical Implications

From the standpoint of the breeder or silviculturist, the dominant female influence on conelet drop in *P. strobus* implies that individual tree selection for cone retention is of critical importance, especially for seed orchards. Past performance is a good indication of future cone yield. This criterion must, of course, be integrated into the overall selection index and not made at the expense of desirable tree characteristics.

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