Species Hybridization in the Hard Pines, Series Sylvestres

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Introduction

The series *Sylvestres* (= Lariciones) includes Scotch pine (Pinus sylvestris L.), red pine (P. resinosa AIT.), Austrian pine (P. nigra ARN. var. *austriaca* (HOESS) ASCHERS. and GRAEBN.), Mugo pine (P. *mugo* TURRA), Japanese black pine (P. thunbergii PARL.), Japanese red pine (P. densiflora SIEB. and Zucc.) and other less well-known species. This series contains the commercially most important hard pines in New England, New York, and Pennsylvania.

Species hybridization work in the series *Sylvestres* began over a century ago, in 1845, with KLOTSCH's attempted crossings of Scotch and Austrian pines. Unfortunately that was a false start because, as DUFFIELD and STOCKWELL (1949) pointed out, KLOTSCH did not realize the importance of the 2 years required for cone development in the pines. He collected his "hybrid" cones the same year he made his pollinations.

Except for taxonomic descriptions of natural hybrids and the small pioneer research of BLAKESLEE in 1914 (JOHNSON, 1939), the field of pine species hybridization remained nearly quiescent until 1924, when the Eddy Tree Breeding Station (now the Institute of Forest Genetics of the U. S. Forest Service) was founded at Placerville, California. Workers at the Institute have developed a most complete arboretum of pine species and have produced numerous species hybrids, contributing greatly to our knowledge of the genetics of the genus. Among the many articles published by Institute workers, the following deal with the series *Sylvestres:* RIGHTER and DUFFIELD (1951); DUFFIELD (1932).

Workers at the Northeastern Forest Experiment Station initiated work on hybridization with the series *Sylvestres* in 1937 at New Haven, Connecticut. The second World War interrupted that work in 1941. It was resumed in 1946 at Philadelphia, Pennsylvania. Previously published references to this Station's work on these hybrids are: SCHREINER (1949); WRIGHT (1953, 1956); and ANONYMOUS (1955).

Interspecific hybridization in the series *Sylvestres* has attracted sporadic attention from other workers in America (JOHNSON and HEIMBURGER, 1946) and in Europe (LIESE, 1926; WETTSTEIN, 1951; and SCHMIDT, 1956). Recently Asiatic workers (NOHARA, ZINNO, and ITO, 1951; HYUN, 1956) started intensive work in this series.

There are several reasons for our continuing interest in species hybridization in the series *Sylvestres.* First, several of the hybrids have been produced in such quantities and have grown so rapidly in the nursery that mass-production of heterotic F_1 hybrids appears practical. Second, the species hybrids can combine the best characteristics of two different species. Third, determination of the crossability pattern should throw light on the formation of races and species. And last, the hybridization work can contribute fundamental knowledge to genetics, taxonomy, and ecology.

This paper is a progress report on the Northeastern Forest Experiment Station's studies in species hybridization in the series *Sylvestres* from 1948 to 1956. It includes data on crossability patterns and on the nursery growth of the hybrids. The data on crossability patterns are more final than are those on growth.

Materials

The female parents used in these crossing experiments were planted specimens of unknown provenance located in the Morris Arboretum of the University of Pennsylvania, Philadelphia; Haverford College Arboretum, Haverford, Pennsylvania; Westtown School Arboretum, Westtown, Pennsylvania; Andorra Nursery, Conshohocken, Pennsylvania; and in various private yards in the vicinity of Ambler, Pennsylvania.

Many of the female parents were also used as male parents. In addition, pollen was obtained from trees growing in the Eddy Arboretum of the Institute of Forest Genetics, Placerville, California; from F_1 hybrids (P. nigra X densiflora) produced in 1914 by A. F. BLAKESLEE and now growing on Long Island, New York (JOHNSON, 1939); and from F_1 hybrids (P. thunbergii X densiflora and P. densiflora X sylvestris) produced by E. J. SCHREINER and others at the Northeastern Forest Experiment Station during the period 1937 to 1941.

All together, we attempted self-pollinations in five species, intraspecific cross-pollinations in six species, four backcross combinations, and 51 different combinations (including reciprocals) between species or species hybrids. Descriptions of the parent species follow:

Red Pine (Pinus resinosa Ait.)

Red pine grows naturally from West Virginia north to the maritime provinces of Canada and west to North Dakota. It has been commonly planted in Philadelphia and elsewhere in the Northeast because of its rapid growth rate and excellent bole form. However, it is susceptible to the European pine shoot moth (Rhyacionia buoliana (SCHIFF.)), and without control of that pest it cannot be used in the warmer parts of Pennsylvania, New York, and New England.

Red pine was used in the controlled pollination experiments from 1947 to 1950. In 1949, when nearly all trees flowered, it was possible to bag 30 to 40 female strobili on each parent tree. In the other years flowering was light, and trees that bore only 5 to 10 female strobili were used as female parents.

Scotch Pine (P. sylvestris L.)

Scotch pine, which occurs naturally in most parts of Europe, is a rapidly growing tree of excellent bole form when grown from seed of the proper provenance. It is common in the Philadelphia area. Most of the trees used in our experiments are believed to be of straight-stemmed Latvian provenances.

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The Scotch pines used as female parents produced about the same quantity of flowers year after year. As many as 40 pollination bags were sometimes applied to heavily flowering trees, each bag enclosing 2 to 4 female strobili.

Japanese Red Pine (P. densiflora Sieb. and Zucc.)

The Japanese red pine grows at higher altitudes in Japan than does the Japanese black pine, and it is proving to be hardier in the Northeast than the latter species. Like the Japanese black pine, it fruits at an early age and reproduces naturally whenever given the opportunity. This natural reproduction is very fast-growing and is straight, in contrast to the planted specimens, which are usually crooked and short. In spite of the fact that many of the Japanese red pines flowered abundantly, this species was difficult to use as a female parent. Occasionally there was complete flower-bud mortality (presumable due to insect damage), which became apparent between the time of bagging and the time of receptivity. Some of the smaller trees used as female parents matured only partially developed cones.

Chinese Pine (P. tabulaeformis Carr.)

The Chinese pine (*P. tabulaeformis* CARR.) has an extensive range in western China. It is an extremely variable species — perhaps as variable as Scotch pine. The four Philadelphia specimens used as parents represent at least three different geographic ecotypes. Two are table-topped and stiff-needled, and have red male catkins; one is tall-growing and stiff-needled and has red male catkins; the other is tall-growing and fine-needled and has yellow male catkins. In some years it was possible to apply 20 or 30 three-strobilus bags to each of the tall-growing specimens. However, this species was difficult to use as a female parent because of the very low sets of filled seeds.

Austrian Pine (P. nigra Arn. var. Austriaca (Hoess) Aschers. and Graebn.)

Austrian pine is a variety of *Pinus nigra* from Austria. It is straight-boled, coarsely branched, and moderately fast growing. It is common in Philadelphia, and is starting to be used in forestry plantings. Unfortunately the other varieties of this species, some of which are superior to Austrian pine in growth rate and fineness of branch, are not available in Philadelphia.

Austrian pine trees flower at frequent intervals. In most years it was easy to locate many 30- to 40-foot specimens on each of which 15 to 25 pollination bags could be placed. Each pollination bag enclosed 2 to 5 female strobili; frequently none of the conelets matured.

Japanese Black Pine (P. thunbergii Parl.)

Japanese black pine is, in Japan, the better formed of the two Japanese hard pines and is commonly used for reforestation in that country. It has been planted most extensively in Long Island because of its resistance to salt spray. It fruits at a very early age, and plentiful natural reproduction is found around at least two groups of suitably situated parents near Philadelphia. This natural reproduction is straight (at least up to 20 feet tall) whereas the older planted trees are crooked and subject to lean. The species is proving non-hardy in the Berkshire Mountains of western Massachusetts and the Allegheny Plateau of northwestern Pennsylvania.

Japanese black pine was the most reliable of all species for use as a female parent. On occasional trees it was possible to enclose 400 female strobili in 25 pollination bags. None of the female parents suffered high cone mortality.

Other Species

Masson pine (*P. massoniana* LAMB.) is a fine timber tree from southwestern China. It proved non-hardy its first winter in one test at Philadelphia. *P. yunnanensis* FRANCH., from Yunnan Province, China and Formosa pine (*P. taiwanensis* HAYATA) from Formosa, are also important timber trees in their native regions but are probably non-hardy in this region. Workers at the Institute of Forest Genetics forwarded pollen of these three species for use in our experiments.

The following species belonging to the series *Sylvestres* were not used in the crossing work: Tropical pine (*P. tropicalis* MORELET); Luchu pine (*P. luchuensis* MAYR); Luzon pine (*P. insularis* ENDL.); Merkus pine (*P. merkusii* DE VRIESE); Heldreich pine (*P. heldreichii* CHRIST); and mugo pine.

Male Flowering Habits and Phenology

In all species used, almost every tree of fruiting size produced an abundance of pollen every year.

Depending on the earliness of the season, these hard pines bloomed from early to late May in Philadelphia. The period of apparent receptivity usually lasted 3 to 5 days in a single species, and about 2 weeks for the series as a whole. The order of blooming was as follows: first Chinese pine, then Japanese black pine, Scotch pine, Japanese red pine, red pine, and Austrian pine.

The Scotch and Japanese red pines have similar enough blooming periods that it is possible to make reciprocal crosses easily. This is also true of the group that includes red and Austrian pines. On the other hand, it is necessary to search for exceptionally early trees of Japanese black, Japanese red, or Austrian pines when it is desired to use fresh pollen of these species on Chinese, Japanese black, or Japanese red pine females respectively.

Methods

The flowering branches were bagged with synthetic sausage casings when the flower buds were in stage I (flower buds expanded, female strobili not yet visible). The pollinations were made and the branches were labelled 1 to 2 weeks later, when the female strobili were in stage V (scales and bracts equal in size, scales widely separated). After another interval of 1 to 2 weeks, when the flowers were in stage VII (scales grown together, bracts no longer visible), the pollination bags were removed. The cones were collected 3 to 4 days before the normal cone-opening date.

Domestic pollens were collected from nearly-ripe catkins which were allowed to shed on paper in the laboratory. The pollen was sieved, dried a few hours, and stored until used at 24 percent relative humidity and 40^0 F. Most pollens were used within 3 days of their extraction date.

The seeds were extracted at air temperature, cleaned, and sorted into "empties" (light) and "fulls" (dark) by color or by flotation in ethyl alcohol (necessary only in Austrian pine). The seeds were stored dry in a refrigerator and were stratified in cold water for 2 weeks before sowing.

Prior to 1954 all the control-pollinated seeds were germinated in a greenhouse and transplanted when a few weeks old to replicated nursery plots. In 1954 and later years the seed was sown directly into unreplicated nursery beds at a density of 40 seeds per square foot. Most of the trees were scored for hybridity and outplanted as 2-0 stock. Because most species × species combinations were represented by several seedlots, it was possible to reach valid conclusions regarding the significance of parentage differences in spite of the lack of replication of the individual seedlots.

The seedlings resulting from pollinations in 1953 and earlier years have been established in permanent test plantations in the following localities: Alfred, Maine; Williamstown, Massachusetts; Paul Smiths, New York; Valhalla, New York; Washington Crossing, New Jersey; Lebanon State Forest, New Jersey; Johnsonburg, Pennsylvania; Philadelphia, Pennsylvania; Kennett Square, Pennsylvania; Paoli, Pennsylvania; Beltsville, Maryland; and Howard County, Maryland.

Results

Species Crossability Pattern

Our species crossing work in the series *Sylvestres* is summarized in table 1. A perusal of that table indicates that there is little or no relationship between the set of filled seeds per cone set or set of empty seeds per cone. For example, the cross *P. silvestris* × *densiflora* gave higher cone sets and empty seed sets than did any other cross on *P. sylvestris* female, yet yielded no filled seeds. Apparently the fact that a given cross yields large quantities of empty seeds means simply that the parent species are closely enough related that pollen of one species can stimulate seed-coat development in the other, and not that the cross will yield filled seeds if attempted again.

Japanese black pine was used as a female parent in 10 different interspecific combinations involving 86 different tree × tree combinations. These may be broken down as follows:

1 species × species combination (8 tree × tree combinations) yielded no filled seed.
9 species × species combinations yielded filled seed. These include:
68 tree × tree combinations that yielded filled seed, and
10 tree × tree combinations that yielded no filled seed.

In the successful species × species combinations the average tree × tree combination involved 1430/78 or 18.3 flowers and has a 10/78 probability of not yielding filled seeds. There was a $(10/78)^2$ or 0.0164 probability that two tree × tree combinations (involving 36.6 female flowers) between crossable species would yield no filled seeds.

Similar methods of calculation were used to determine the reliability of the crossability information in three other species. The calculations for Austrian and Japanese red pines were based on data from interspecific crosses; the calculations for Scotch pine were based on data from intraspecific crosses. When using Austrian pine as a fe-

Table 1. — Summary of series *Sylvestres* interspecific hybridizations at the Northeastern Forest Experiment Station, 1948 to 1956

Female parent, *Pinus* —	Male parent, *Pinus* — wind	self	*resinosa*	*thunbergii*	*densiflora*	*tabulaeformis*	*yannanensis*	*taiwanensis*	*massoniana*	*nigra* var. *austriaca*	*sylvestris*	*thunbergii* × *densiflora*	*nigra* × *densiflora*	*densiflora* × *sylvestris*
resinosa	68	—	25	137	128	141	125	130	131	268	131	—	—	—
	79	—	28	14	19	15	17	16	18	19	16	—	—	—
	1.5	—	7.6	.9	.4	.1	.1	.1	.1	.2	.1	—	—	—
	1.2	—	8.0	.0	.0	.0	.0	.0	.0	.0	.0	—	—	—
thunbergii	1653	140	—	81	397	346	40	259	24	26	89	294	44	—
	86	44	—	59	65	83	70	68	42	100	59	58	68	—
	7.2	11.6	—	7.1	10.5	18.5	14.0	15.3	30.3	23.1	16.9	8.4	18.0	—
	12.3	10.7	—	26.2	11.7	8.9	21.8	1.0	12.1	0.4	0.0	21.2	0.5	—
densiflora	882	44	30	173	32	19	—	175	65	45	325	47	—	3
	63	36	74	43	31	26	—	65	54	38	47	55	—	100
	13.7	3.2	18.3	9.3	26.9	.0	—	.2	5.3	6.7	16.8	3.7	—	7.0
	8.1	1.5	.0	1.2	55.2	.0	—	.3	.0	7.8	.3	9.3	—	11.1
tabulaeformis	853	53	3	193	10[1])	78	31	27	32	14	50	11	—	—
	87	38	100	31	50	51	3	8	12	7	26	0	—	—
	4.3	.2	8.0	2.9	1.2	1.9	2.0	.0	.0	.0	5.6	—	—	—
	.8	.1	.0	.1	.0	.4	.0	1.5	.0	.0	.0	—	—	—
nigra var. *austriaca*	1652	11	61	369	385	140	32	47	10	160	54	183	—	66
	69	9	20	41	40	25	9	11	30	24	22	22	—	29
	10.7	8.0	13.1	7.1	5.0	4.6	17.3	2.4	.0	7.1	12.3	5.8	—	18.7
	9.8	.0	.0	1.5	5.9	.5	.0	3.4	.0	23.0	.0	3.8	—	6.1
sylvestris	999	30	94	49	109	96	16	32	14	73	113	18	—	41
	52	6	21	26	56	18	19	12	28	54	30	61	—	67
	2.8	.5	.1	4.7	12.1	2.2	.0	1.5	10.2	8.3	3.5	10.1	—	3.6
	2.3	.0	.0	.0	.0	.0	.0	.0	.0	.2	6.8	.1	—	5.3

Legend:
25 Strobili pollinated.
28 Cone set, percent.
7.6 Empty seeds per cone.
8.0 Full seeds per cone.

[1]) Year-old pollen was used.

male parent there was a probability of 0.0178 that seven different tree × tree combinations (involving 104.3 female flowers) between crossable species would yield no filled seed. The corresponding figures for Japanese red pine are four tree × tree combinations (involving 99.2 female flowers) and a probability of 0.0159; for Scotch pine they are seven tree × tree combinations (involving 56.5 female flowers) and a probability of 0.0198. According to these probability figures, several crosses listed as failures in table 1 might have succeeded if tried in sufficient quantity. All reported species crosses within the series are summarized in table 2.

Righter and Duffield (1951), and Duffield (1952) reported failures for the numerous inter-series hybridizations involving the series *Sylvestres* attempted at the Institute of Forest Genetics. Schmidt (1956) reported several failures and some successes (*P. sylvestris* × *patula*, *P. s.* × *radiata*, *P. s.* × *pinaster*, and *P. s.* × *palustris*) in inter-series hybridizations involving Scotch pine. However, he did not include seed-set data, descriptions of the putative hybrids, nor authorities for the scientific names used. Nohara, Zinno, and Ito (1951) reported the successful crossing of *Teidamatsu* (= *P. taeda* L.) and *Akamatsu* (= *P. densiflora*); they reported failures for the crosses *Akamatsu* × *Daiōmatsu* (= *P. palustris* Mill.?), *Kuromatsu* (= *P. thunbergii*) × *Teidamatsu*, and *Kuromatsu* × *Daiōmatsu*. Hyun (1956) reported a failure for the cross *P. rigida* Mill. × Japanese red pine.

Nursery Performance of the Hybrids

The crosses *P. tabulaeformis* × *thunbergii*, and *P. sylvestris* × (*thunbergii* × *densiflora*) resulted in very small numbers of presumably filled seeds that either did not germinate or gave seedlings that were indistinguishable from the female parents. Therefore these crosses are presumed to be failures. The cross *P. nigra* × (*densiflora* × *sylvestris*) resulted in moderate numbers of filled seeds, which have not yet been sown in the nursery. It is considered as probably successful.

Table 2. — Summary of all species hybridization in the series *Sylvestres*

Female parent, *Pinus* —	Male parent. *Pinus* —													
	American species	Asiatic species							European species			Hybrids		
	resinosa	*thunbergii*	*densiflora*	*tabulaeformis*	*yunnanensis*	*taiwanensis*	*massoniana*	*insularis*	*nigra*	*mugo*	*sylvestris*	*thunbergii* × *densiflora*	*nigra* × *densiflora*	*densiflora* × *sylvestris*
American species														
resinosa	H 13, 14	F 13, 14	F 13, 14	F 14	F 14	F 14	F 14	—	U 6 F 14	F 13	F 13, 14	—	—	—
Asiatic species														
thunbergii	U 6 F 1, 13	H 9 13, 14	H 7, 12 13, 14	H 12, 14	H 14	H 14	H 14	—	H 14	—	F 13, 14	H 7, 14	H 14	—
densiflora	F 13, 14	H 7, 13, 14	H 13, 14	F 12, 14	—	H 14	H 14	—	H 14	F 13	H 13, 14	H 7, 14	—	H 14
tabulaeformis	F 14	F 14	—	H 14	F 14	H 14	F 14	H 11	F 14	—	F 14	F 14	—	—
European species														
nigra	F 1, 6, 14	F 1, 6 H 14	H 2, 14	H 14	F 14	H 14	F 14	—	H 6, 14	—	H 3, 10 F 1, 14	H 14	—	U 14
mugo	F 13	F 13	F 13	—	—	—	—	—	—	—	F *4 H 2,5	—	—	—
sylvestris	F 1, 6, 8 13, 14	F 1, 6 13, 14	F 13, 14	F 14	F 14	F 14	F 14	—	U 3 H 2, 8, 14	F 3, 4 H 2, 5	H 9 13, 14	F 14	—	H 14

Legend: H = Hybrids obtained.
U = Unkown. Full seeds obtained but hybrids not yet authenticated.
F = Failure.
* = Natural hybrid, direction of cross unknown.

Authorities

1. Duffield, 1952.
2. Johnson, 1939.
3. Johnson and Heimburger, 1946.
4. Liese, 1927.
5. Rehder, 1940.
6. Righter and Duffield, 1951.
7. Saito, 1951.
8. Schmidt, 1956.
9. Schreiner, 1949.
10. Wettstein, 1951.
11. Wu, 1956.
12. Hyun, 1956.
13. Northeastern Forest Experiment Station, 1937—1941, unpublished data.
14. Present studies.

Following is an annotated list (based on second-year nursery performance unless otherwise indicated) of the authenticated species combinations. In each case the female parent is listed first. The characteristics that are of sufficient value to permit the identification of single seedlings as hybrids are italicized.

P. thunbergii × self. Trees 50 to 90 percent as tall as crossed *P. thunbergii.*

P. thunbergii × *densiflora.* Trees with lammas shoots and up to *50 percent taller* than *P. thunbergii; buds brown,* slightly smaller than in *P. thunbergii; needles 10 to 14 centimeters long* (7 to 8 centimeters long in *P. thunbergii),* greener than in *P. thunbergii.* The probable heterosis and high seed sets mark this as one of the most promising species combinations for the Northeast.

P. thunbergii × *tabulaeformis.* Trees 10 to 30 percent slower growing than *P. thunbergii; buds tan; first-year buds hidden by needles;* bud scales loosely appressed; *first-year needles purple-green; second-year needles 12 to 13 centimeters long,* of medium coarseness.

P. thunbergii × *taiwanensis.* First-year seedlings about *20 percent* taller than *P. thunbergii; buds tan, with loosely appressed scales,* 5 to 7 millimeters in diameter (4 to 5 millimeters in *P. thunbergii);* needles moderately coarse, *11 to 17 centimeters long.*

P. thunbergii × *yunnanensis.* Trees slightly faster growing than *P. thunbergii; buds tan, 6 to 7 millimeters in diameter; primary (first-year) needles very serrate and 36 to 45 millimeters long* (18 to 24 millimeters long in *P. thunbergii);* secondary needles 8 to 12 centimeters long, *three per fascicle.*

P. thunbergii × *massoniana.* Second-year seedlings 30 to 60 percent taller than *P. thunbergii;* buds tan; *primary needles 30 to 40 millimeters long;* secondary needles yellow-green, 10 to 11 centimeters long, *fine.*

P. thunbergii × *nigra* var. *austriaca.* Trees without lammas shoots, slightly faster growing than *P. thunbergii; buds 7 millimeters in diameter; primary needles 33 to 44 millimeters long; secondary needles very coarse and dark green.*

P. thunbergii × *(thunbergii* × *densiflora).* Seedlings slightly faster growing than *P. thunbergii; buds light tan;* needles 8 to 14 centimeters long.

P. thunbergii × *(nigra* × *densiflora). Buds light brown,* slightly larger than in *P. thunbergii;* needles 10 to 16 centimeters long, darker green than in *P. thunbergii.*

P. densiflora × self. Slower growing (by 10 to 20 percent) than crossed *P. densiflora.*

P. densiflora × *thunbergii.* Seedlings slightly faster growing than *P. densiflora, buds tan;* bud scales slightly appressed (very loose at the tips in *P. densiflora);* needles 12 to 13 centimeters long (8 to 12 centimeters long in *P. densiflora).*

P densiflora × *taiwanensis.* Hybridity probable. Primary needles longer, and bud scales more appressed at tip than in *P. densiflora.*

P. densiflora × *massoniana.* Hybridity probable. Seedling taller than *P. densiflora;* needles fine; buds light brown, 4 millimeters in diameter (3 millimeters in *P. densiflora).*

P. densiflora × *nigra* var. *austriaca.* Most seedlings without lammas shoots, 10 to 20 percent slower growing than *P. densiflora, buds light brown, resinous, 4 to 5 millimeters in diameter; bud scales appressed;* needles 12 to 17 centimeters long.

P. densiflora × *sylvestris.* Seedlings taller than in *P. densiflora; buds resinous, light brown; needles 13 to 15 centimeters long,* coarser than in *P. densiflora.* Older trees of this combination grew more rapidly than either parent (Schreiner, 1949).

P. densiflora × *(thunbergii* × *densiflora).* Bud scales more appressed than in *P. densiflora.*

P. densiflora × *(densiflora* × *sylvestris).* First-year buds light brown, hidden by needles; first-year needles green (slight purple tinge in *P. densiflora).*

P. tabulaeformis × *taiwanensis. Needles yellow-green,* fine; buds darker brown than in *P. tabulaeformis.*

P. nigra var. *austriaca* × *thunbergii.* Seedlings with lammas shoots, *20 to 28 centimeters tall* (7 to 16 centimeters in *P. nigra* var. *austriaca);* buds white, 6 millimeters in diameter (7 millimeters in *P. nigra* var. *austriaca); secondary needles formed early the first year.*

P. nigra var. austriaca × *densiflora. Buds 5 millimeters in diameter;* seedlings with lammas shoots, *15 to 22 centimeters tall.* Putative natural hybrids of this combination have been identified in four wind-pollinated progenies of isolated *P. nigra* var. *austriaca* trees situated close to *P. densiflora* trees in bloom at the same time. Te ease of natural hybridization, the consistent and relatively high seed sets to controlled pollination, and the rapid juvenile growth mark this as one of the most promising hybrid combinations.

P. nigra var. *austriaca* × *tabulaeformis. Leaves yellow-green,* shorter than in the female parent; trees taller than *P. nigra* var. *austriaca.*

P. nigra var. *austriaca* × *taiwanensis. Needles 14 centimeters long* (9 to 13 centimeters in *P. nigra* var. *austriaca);* trees with lammas shoots, 13 to 17 centimeters tall.

P. nigra var. *austriaca* × *(thunbergii* × *densiflora* natural hybrid). *Faster growing than female parent.* Most seeds of this combination have not yet been sown in the nursery.

P. sylvestris × *nigra* var. *austriaca.* Buds slightly larger and lighter than in *P. sylvestris;* trees 25 percent shorter than *P. sylvestris.*

P. sylvestris × *(densiflora* × *sylvestris).* Taller than *P. sylvestris.*

Fresh Versus Year-Old Pollen

It was sometimes necessary to use year-old pollen stored at 25 to 50 percent relative humidity at 35° to 40° F., as recommended by Duffield (1954), in order to pollinate an early-blooming female with a late-blooming male. Over a period of 4 years the year-old pollen was used on a total of 1,132 female flowers, yielding 675 cones. The differences in cone set and set of empty seeds per cone for fresh and year-old pollen were slight, and often in favor of the year-old pollen. However, in most cases the sets of filled seeds were much less with year-old than with fresh pollen (table 3), indicating that fresh pollen should be used if at all possible.

Duffield and Snow (1941) and Duffield (1954) have shown that properly stored pine pollen retains its ability to germinate in artificial media for more than a year. The difference between their *in vitro* results and our *in vivo* results is probably due to the long interval between pollination and fertilization in the pines. The year-old pollen evidently retained sufficient viability to germinate after pollination and to result in seed-coat formation, a phe-

Table 3. — Numbers of full seeds per cone following pollination with fresh and with year-old pollen[1])

Female × male parent, *Pinus* —	Fresh pollen	Year-old pollen
thunbergii × *thunbergii*	26.2	7.2
thunbergii × *densiflora*	11.7	2.1
thunbergii × *(thunbergii* × *densifora)*	21.2	2.9
thunbergii × *tabulaeformis*	8.9	2.1
thunbergii × *nigra*	.4	.7
densiflora × *densiflora*	55.2	1.3
densiflora × *sylvestris*	.3	.0
nigra × *nigra*	23.0	.0
nigra × *densiflora*	5.9	2.1
nigra × *(thunbergii* × *densiflora)*	3.8	3.0

[1]) The fresh and year-old pollens were usually collected from different trees.

nomenon that occurs before ovule fertilization in pine (Buchholz, 1946). But it seemed to have lost enough vitality to be incapable of fertilizing the ovule after a further 12- to 13-month stay in the female strobile.

The Next Steps

We have determined the main features of the crossability pattern in the series *Sylvestres* and have learned something about the nursery performance of the species hybrids. But much remains to be done before the results of these studies can be applied on a large scale.

There are at least 15 to 20 years of testing ahead before any one of the hybrids can be recommended for general use on a large scale. This testing should be done in several different areas if we are to determine the proper niche for each combination. At present, the establishment of good test plantings is time-consuming and expensive, requiring a great deal of labelling and record-keeping. As more of the easily identifiable hybrids become available, the expense of testing can be reduced considerably by the establishment of unlabelled "bucket-mix" plantings.

The crossability chart could be extended to include the other species in the series *(P. tropicalis, P. luchuensis, P. insularis, P. merkusii,* and *P. heldreichii)* whose genetic relationships have not been studied. This extension does not deserve high priority in the Northeast because the hardiness of these species is doubtful.

We used whatever individuals and ecotypes were easily available as parents. No attempts were made at selection. It would be desirable to repeat the most promising combinations, using selected ecotypes and individuals as parents.

The most successful species combination was *P. thunbergii* × *densiflora,* of which we harvested slightly more than 3,000 filled seeds at a cost of a few cents per seed. Special studies of mass-production techniques will be necessary to lower the cost for large-scale reforestation work.

The cross *P. densiflora* × *sylvestris* is very promising for growth but not for mass-production purposes. The answer may lie in the use of F_2 seed produced in orchards of grafted F_1 trees. That can be determined only by producing and testing numerous F_2 hybrids.

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Summary

Fifty-five species crosses (including reciprocals and backcrosses) of the hard pines series *Sylvestres* were attempted at the Northeastern Forest Experiment Station during the period 1948 to 1956. Thirty-one of these crosses were failures; one was probably successful; and 23 yielded hybrids that have been authenticated in the nursery or in permanent test plantings. The American *Pinus resinosa* failed to cross with any other species. The Japanese *P. thunbergii* and *P. densiflora* crossed easily with each other and with several Chinese and Formosan species. Crosses between the European *P. nigra* and *P. sylvestris* yielded a few hybrids, as did the crosses involving a European and a Japanese species.

Two-year-old seedlings of *P. thunbergii* × *densiflora, P. thunbergii* × *taiwanensis, P. thunbergii* × *massoniana, P. thunbergii* × *nigra* var. *austriaca, P. densiflora* × *thunbergii, P. densiflora* × *sylvestris, P. nigra* var. *austriaca* × *thunbergii,* and *P. nigra* var. *austriaca* × *densiflora* were taller than non-hybrid seedlings from the same female parents. Descriptions of the diagnostic characteristics of these and other hybrid combinations are reported.

Selfed progenies of *P. thunbergii* and *P. densiflora* were markedly smaller than crossed progenies of these species.

Cone sets and sets of empty seeds were as high with year-old pollen as with fresh pollen. However, the sets of filled seeds were much less with the year-old pollen than with fresh pollen.

Résumé

Titre de l'article: *Hybridation interspécifique chez les pins, section Sylvestres.*

55 croisements interspécifiques (y compris des croisements réciproques et croisements en retour) dans la section *sylvestres* furent essayés à la Northeastern Forest Experiment Station de 1948 à 1956. 31 de ces croisements ont échoué; un réussit probablement, et 23 ont produit des hybrides identifiés en pépinière ou dans des plantations d'essai permanentes.

Le pin américain *P. resinosa* ne peut être hybride avec aucune autre espèce. Les pins japonais *P. thunbergii* et *P. densiflora* se croisent facilement l'un avec l'autre et avec plusieurs espèces de Chine et de Formose. Les croisements entre les pins européens *P. nigra* et *P. sylvestris* ont donné quelques hybrides, de même que les croisements comprenant un parent européen et un japonais.

Les croisements suivants, en semis de deux ans, sont plus grands que les semis non-hybrides du même parent femelle: *P. thunbergii* × *P. densiflora, P. thunbergii* × *P. taiwanensis, P. thunbergii* × *P. massoniana, P. thunbergii* × *P. nigra* var. *austriaca, P. densiflora* × *P. thunbergii, P. densiflora* × *P. sylvestris, P. nigra* var. *austriaca* × *P. thunbergii, P. nigra* var. *austriaca* × *P. densiflora.* Les caractères distinctifs de ces hybrides et d'autres croisements sont énumérés.

Des descendants autofécondés de *P. thunbergii* et *P. densiflora* sont nettement plus petits que les descendants hétérofécondés de ces espèces.

La production de cônes et de graines vides est aussi élevée avec du pollen de un an qu'avec du pollen frais. Cependant, le pollen conservé un an donne beaucoup moins de graines pleines que le pollen frais.

Zusammenfassung

Titel der Arbeit: *Artkreuzungen innerhalb der „Hartkiefern", Reihe Silvestres.*

Von 1948 bis 1956 wurden in der Northeastern For. Expt. Station 55 Artkreuzungen (inkl. Rück- und Reziprokkreuzungen) innerhalb der Reihe *Silvestres* durchgeführt. Davon mißlangen 31, eine war wahrscheinlich, 23 waren mit Sicherheit erfolgreich. *P. resinosa* ließ sich mit keiner anderen Art kreuzen. *P. thunbergii* und *P. densiflora* waren leicht miteinander und mit einigen chinesischen und formosischen Arten zu kreuzen. *P. nigra* × *P. silvestris,* wie auch die Kreuzung zwischen einer der beiden japanischen und einer dieser europäischen Arten erbrachten nur wenige Bastarde.

2jährige Sämlinge der Kreuzungen *P. thunbergii* × *densiflora, P. thunbergii* × *taiwanensis, P. thunbergii* × *massoniana, P. thunbergii* × *nigra* var. *austriaca, P. densiflora* × *thunbergii, P. densiflora* × *silvestris, P. nigra* var. *austriaca* × *thunbergii* und *P. nigra* var. *austriaca* × *densiflora* waren höher als normale Nachkommen der gleichen Mutterbäume. Die diagnostischen Merkmale dieser und anderer Hybriden werden beschrieben. Selbstungsnachkommen von *P. thunbergii* und *P. densiflora* wachsen deutlich langsamer als Fremdungen.

Zapfenansatz und Hohlkorngehalt waren bei der Verwendung von 1jährigen und frischen Pollen gleich hoch. Wesentlich geringer liegt jedoch der Gehalt an vollen Samen, wenn man mit 1jährigen Pollen stäubte.

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