apres la fin du traitement au iroid le 27 Novembre (822 heures au-dessous de 7° C); cependant, le debourrage d'un arbre dc la provenance Ohio etait anormal et limité aux bourgeons inférieurs.

La lcngueur de la periode de dormance apres l'exposition au froid variait a la fois avec l'intensité du froid et avec la provenance. Plus intense etait la refrigeration, plus courte la periode suivante avant le debourrage. Les différences entre les ecotypes septentrionaux et méridionaux en ce qui concerne la longueur de cette pkriode de dormance ont diminue avec l'augmentation de l'intensité du froid. Lorsque la refrigeration etait terminee en fin Janviei ou au début Février, il y avait tres peu de différence dans la durée de la dormance apres réfrigération entre les écotypes septentrionaux et meridionaux.

L'efficacité de l'augrnentation de réfrigération pour réduire la période de dormance avant le debourrage n'était pas toujours la même. En ce qui coneerne les proveances de Géorgie, la reduction maxima est intervenue apres environ 300 heures d'exposition au-dessous de 7° C. Pour les provenances du Tennessee, la reductinn fut presqu'aussi importante apres 1200 et 1600 heures qu'apres 400 heures. Pour les arbres de l'Ohio et du Michigan, la réduction maximum est intervenue après 1600 heures au-dessous de 7° C.

L'augmentation de l'intensité du froid augmente la vitesse de débourrage en diminuant le nombre de jours entre le stadc 1 et le stade 6. La réfrigération au-dela de debut Février (environ 2300 heures au-dessous de 7° C) ne semble plus avoir d'effet sur l'augmentation de la vitesse de deborrage même chez les arbres d'origine septentrionale

Les abres cxposes a l'hiver normal dans la plantation comparative en Ohio ont débourré de la façon suivante: les provenances scptentrionales les premières et les provenances méridionales les dernieres; toutes, suivant une variation clinale.

Pour ies armes exposes a l'hiver dans la plantation comparative de Floride centrale (environ 400 heures audcssous de 7° C), les provenances de Géorgie ont debourre les premieres; les autres provenances ont debourre des provenances de Géorgie a été la même à l'exterieur en Floride et en Ohio, mais pour les ecolypes septentrionaux, cette durée etait beaucoup plus courte en Floride qu'en Ohio.

Lette étude montre qu'apre la mi-Février, dans les conditions de l'essai (environ 2500 heures au-dessous de 7° C), les besoins en froid des arbres de toutes les origines ont ete pleinement satisfaits et que d'autres facteurs ont déterminé l'époque de débourrage.

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lnterspecific Hybridization in the Genus Abies

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Introduztion

Artificial hybridization is an important tool in forest genetics. It makes it possible to produce trees with gene combinations that might never occur in nature. Tree breeders around the world have placed special emphasis on interspecific crosses of species in various genera. Fairly detailed information on crossability patterns are available for genera such as Pinus, Picen and Larix. Several lists of species crosses in Abies have been reported by workers (JOHNSON, 1939; WRIGHT, 1962[1]); ROHMEDER, 1959 and 1961). However, a search of the literature revealed no current crossability pattern for that genus.

Experiments were initiated in the spring of 1960 at the State University College of Forestry at Syracuse University in an attempt to establish a crossability pattern in Abies. The objectives of this study are as follows:

1. The compilation of reported Abies crosses into a pattern.
2. The extention of this established pattern by experimental artificial hybridization.
3. The production of interspecific hybrids for future study and evaluation for forestry purposes.

This paper reports the results of the controlled pollinations attempted in 1960 along with the compiled crossability pattern. The results of new crosses carried out in 1962 and data on the putative hybrids produced in 1960 will be reported at a later date.

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[1]) Personal communication, J. W. WRIGHT, Michigan State University, East Lansing, Michigan (2/28/62).

Review of Literature

General

SARGENT (1926) recognized 33 species of Abies existing in the temperate regions of the northern hemisphere. VIGUÉ and GAUSSEN (1929) arrived at a total of 52 species and 12 varieties in their revision of the genus. REHDER (1958) lists 31 species, but states that "about 40 species" of true firs exist in the temperate regions of the northern hemisphere.

Various workers have divided the genus Abies into two or three sections. According to MCNAB (1876), Bertrand separated the species into two sections based on the position of the needle resin canals. MATTFELD's (1926) maps divide Mediterranem species into two sections based on

female parent \ male parent		Mediterranean								Asian									North American							
		numidica	pinsapo	nordmanniana	cephalonica	alba	cilicica	nord. x ceph.	nord. x cilic.	pindrow	spectabilis	sibirica	veitchii or var. olivacea	sachalinensis	sachalinensis var. mayriana	homolepis	recurvata	nephrolepis	balsamea	fraseri	concolor var. lowiana	concolor	grandis	nobilis	lasiocarpa	amabilis
Mediterranean	numidica		IS			A																				
	pinsapo	IS		NA	A	NA																				
	nordmanniana		A		IA	NA	A						A									A	A			
	cephalonica			I		I																				
	alba		S	A									A									A	A			
	cilicica																									
	nord. x ceph.								P					P		P						P				
	nord. x cilic.																									
Asian	pindrow		N								N															
	spectabilis									N								N	N							
	sibirica												A													
	veitchii or var. olivacea			A		A		P														A	A			
	sachalinensis				P	P		P									P									
	sachalinensis var. mayriana															A										
	homolepis					A		P														A	A			
	recurvata																									
	koreana												?A													
North American	balsamea			P								N				P				I		P			A	
	fraseri												N						IA							
	concolor var. lowiana																						A			
	concolor			A		A						A	A										NA	A		A
	grandis			A		A							A									A				
	nobilis var. glauca																P									
	lasiocarpa																									S
	amabilis																								S	

Figure 1. Summary of Reported Crosses in Abies

A = artificial cross N = natural cross I = intermediate populations
S = suspected natural cross P = putative artificial cross

the bracts of the cones, which are either longer or shorter than the scales. SARGENT (1898) lists three sections, as determined by ENGELMANN in 1873, based on needle characters. ELWES and HENRY (1909) mention three sections that were proposed by MAYR, based on branch and bud characters. In addition, VEITCH (1881) has combined *A. sachalinensis* and *A. veitchii* into a subsection of the genus. It appears that no satisfactory criteria for dividing the genus into sections have been established. MCNAB, as early as 1876, and REHDER, as late as 1958, have both adopted a geographical arrangement in their respective treatments of the species in *Abies*.

Sympatric fir species exist in western North America, on the islands of Japan, and to some extent in a few areas of the Mediterranean (SARGENT, 1898; HAYASHI, 1951; MATTFELD, 1926). Most species, however, are allopatric — only one species occurring in a given forest region.

The small taxonomic variations between allopatric, as well as sympatric fir species, have caused considerable difficulty. LARSEN (1956) and GATHY (1957) have both attempted to correctly interpret the status of *A. concolor lowiana* in relation to *A. concolor* and *A. grandis* of western United States. MATTFELD (1926), BEISSNER (1909), and REHDER (1958), have described *A. borisii-regis, A. equi-trojani,* and *A. bornmülleriana* as intermediates between or closely related to adjacent species.

Referring to conifers in general, SAX and SAX (1933) point out that differentiation of species seems to be based primarily on genic changes, which, in many cases, do not prevent compatible species hybrids. They believe that many species maintain themselves as distinct units only by geographic or physiological isolation. CHIARUGI (1955) also believes that geographic rather than genetical isolation is responsible for speciation in many tree genera. WRIGHT (1962)[2]) attributes the speciation in fir to geographic rather than genetic isolation.

[2]) Personal communication cited.

Chromosome studies have shown that the basic chromosome number of *Abies* is 12, and that the chromosome morphology of species is very similar, SAX and SAX (1933) have shown that *A. cephalonica* and *A. concolor* both have five of their chromosomes clearly heterobrachial and seven approximately isobrachial. CHIASSON (1962)[3]) has recently begun a study of *Abies* chromosomes, using idograms to show differences between species.

The above review of geographic distribution, taxonomic variation, and genetic structure of the genus *Abies* seems to suggest, as KIELLANDER (1962) and WRIGHT (1962)[4]) have also stated, that fir species should cross readily.

The summary of reported species crosses in *Abies* shows the many crosses occurring in nature and accomplished by man *(Figure 1)*. In addition to this summary, there are two other cases of suspected natural hybrids occurring in North America; *A. magnifica* and *A. procera**) in southwest Oregon (DUFFIELD, 1962),[5]) and *A. balsamea* and *A. lasiocarpa* in northern Alberta, Canada (HEIMBURGER, 1962)[6]).

MERGEN and LESTER (1961) believe that a better knowledge of the floral phenology of the species would result in more successful controlled pollinations. It is possible that with more detailed information on floral development in firs, faulty hybridization methods may be eliminated and genetic compatibility barriers more clearly shown. Only a small share of the attempted crosses in *Abies* have been successful.

Interspecific hybridization in the genus *Abies* appears to have great promise for improvement of fir in North

[3]) Personal communication, L. P. CHIASSON, St. Francis Xavier University, Antigonish, N. S., Canada (1/18/62).

[4]) Personal communication cited.

[5]) Personal communication, J. W. DUFFIELD, Nisqually, Washington (1/16/62).

[6]) Personal communication, C. HEIMBURGER, Maple, Ontario, Canada (1/16/62).

*) *A. procera* synonymous with *A. nobilis;* REHDER (1958) lists *A. nobilis* but lists *A. procera* as being more acceptable in a later edition.

America and in Europe. WRIGHT (1957) has reported many of the exotic fir species as exhibiting faster growth than our native balsam fir. The exotic firs in Rochester, New York, have developed into large trees under conditions which have eliminated the native balsam fir from the collection. DALLIMORE and JACKSON (1923) reported *A. homolepis* as being frost hardy, and *A. firma* and *A. cilicica* as being not as susceptible to some insect attacks as other firs introduced to Great Britain. In addition, both natural and artificial fir hybrids have been reported as exhibiting vigorous growth and being quite fertile (LARSEN, 1956; WRIGHT, 1962[7]); ROHMEDER, 1959 and 1961).

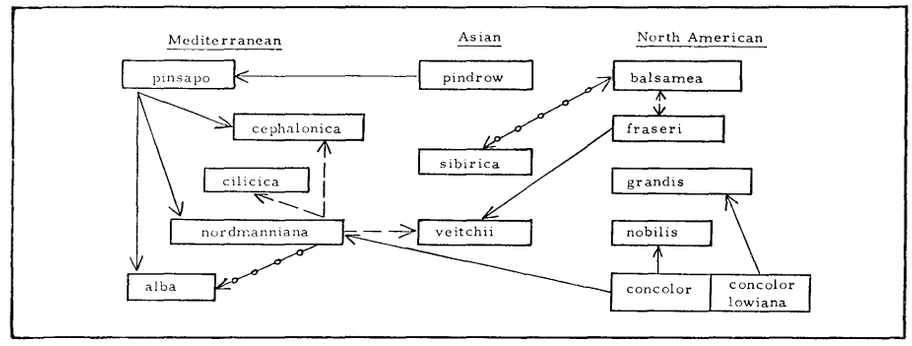

Figure 2. Reported Vigor in Abies Hybrids
(parent species separated into geographical regions)

——→ = hybrids more vigorous than at least one parent
— — → = hybrid vigor not clearly defined
—o—o→ = hybrids less vigorous than parents

(arrows indicate species crosses, with point towards male parent)

The first artificial fir hybrid, *A. pinsapo* × *cephalonica* (*A.* × *vilmorinii* MAST.), has been reported as exhibiting extreme vigor in France (SARGENT, 1898). LARSEN (1956) reports a height of 20.6 m. (67.5 ft.) at age 29 years, for a tree of the artificial hybrid *A. concolor lowiana* × *grandis* growing in Denmark. In the first 12 years from seed, the fastest growing seedling of this cross averaged 1.64 ft. in height per year (LARSEN, 1937). In Germany, ROHMEDER's (1959) artificial hybrids *A. veitchii* × *alba* and *A. concolor* × *cephalonica* have exhibited hybrid vigor in just seven years from seed. In 1961, ROHMEDER stated that in all cases where *A. concolor* was used in a cross, some hybrid vigor was exhibited in the progeny. He states that vigor was most pronounced in those hybrids originating from crosses where the dark-green-needled specimens of *A. concolor* were used as parents. ROHMEDER, however, gives measurements to support hybrid vigor for only one cross involving *A. concolor*. Reports of vigor in *Abies* hybrids have been compiled from the literature and are shown in *Figure 2*.

Some fir hybrids have been reported as being quite fertile. DALLIMORE and JACKSON (1923) reported seedlings being grown from seed of *A.* × *vilmorinii*. The populations of *A. equi-trojani* and *A. bornmülleriana*, both intermediate between *A. nordmanniana* and *A. cephalonica*, have maintained themselves over relatively large ranges in Turkey.

Natural Interspecific Hybrids:

Several natural hybrids or intermediates between species are recognized in the genus *Abies*. In *Table 1* these are listed as occurring within the overlapping ranges of the parent species in natural forests.

Abies borisii-regis is reported by MATTFELD (1926) as being intermediate between and with a range overlapping those of *A. cephalonica* and *A. alba* on the southeast Balkan peninsula. REHDER (1958) lists *A. borisii-regis* as a species related to *A. cephalonica*.

Abies bornmülleriana is given by FLOUS (1936) as a possible hybrid between *A. cephalonica* and *A. nordmanniana*. REHDER (1958) also lists this species as being related to *A. cephalonica*. MATTFELD (1926) shows the range of *A. bornmülleriana* as confined to northwest Turkey and between the ranges of *A. cephalonica* and *A. nordmanniana*.

Abies equi-trojani is presented as a variety of *A. nordmanniana* by DALLIMORE and JACKSON (1923). MATTFELD (1926) describes it as having intermediate characteristics between *A. nordmanniana* and *A. cephalonica*, and covering a small range in western Turkey.

Abies nebrodensis is mentioned by REHDER (1958) as being intermediate between *A. cephalonica* and *A. alba*. DALLIMORE and JACKSON (1923) refer to it as an extremely rare fir of northeastern Sicily. Apparently only a few trees existed as early as 1750.

Abies marocana is said to be intermediate between *A. numidica* and *A. pinsapo* by DALLIMORE and JACKSON (1923), and related to *A. pinsapo* by REHDER (1958). DALLIMORE and JACKSON's statement was based on a specimen found growing in the mountains of Morocco. TURRILL (1955) describes in detail a specimen intermediate between *A. numidica* and *A. pinsapo* growing in an English garden. He states that, "it is a natural variant linking *A. pinsapo* and *A. numidica* or that it is a hybrid between these two morphologically related species."

Table 1. — Natural Forest Interspecific *Abies* Hybrids. — The following crosses show intermediate characters between the species listed and have been described as hybrids, intermediates, and either or both of the species. The first listed parent species is not necessarily the female parent.

Cross	Date, Country of Origin; Date Report.	References*)
1. *A. lasiocarpa* × *amabilis*	w. U.S.; 1898	56, 40
2. *A. balsamea* × *fraseri* (*A. intermedia* FULL.)	e. U.S.; 1936	19, 33
3. *A. numidica* × *pinsapo* (*A. marocana* TRABUT)	Morocco	63, 8, 51, 11
4. *A. cephalonica* × *alba* (*A. nebrodensis* MATTEI.)	Sicily	8, 41, 51
5. *A. alba* × *cephalonica* (*A. borisii-regis* MATTF.)	s. Bulgaria, n. Greece	41, 49
6. *A. normanniana* × *cephalonica* (*A. bornmülleriana* MATTF.)	Turkey	41, 49
7. *A. nordmanniana* × *cephalonica* (*A. equi-trojani* ASCHERS. & SIN.)	Turkey	41, 49
8. *A. sibirica* × *nephrolepis* (*A. sibirico-nephrolepis*)	n. e. China; 1957	61

*) Refer to literature cited for numbered references and sources of reports for specific crosses in *Tables 1, 2, 3,* and *4*. — All species names according to REHDER, 1958.

[7]) Personal communication cited.

Abies intermedia is described by LAMB (1937) as being intermediate between *A. balsamea* and *A. fraseri*. FULLING (1936) recognized it as a true species. It has a limited range in the southeastern Appalachian Mountains of northeastern United States.

SARGENT'S possible hybrid between *A. lasiocarpa* and *A. amabilis* was a single tree which he observed in the Olympic Mountains of western United States. He describes it in general terms of foliage, crown shape, and cone color.

Abies sibirico-nephrolepis is described as a naturally occurring hybrid between *A. sibirica* and *A. nephrolepis*. It occurs in the forests of Tailing in northeastern Heilingkiang Province (TAKENOUCHI and CHIEN, 1957).

The hybrids occurring in arboreta and gardens are listed in *Table 2*. A chronological listing is used in *Table 2*, as in *Tables 1, 3*, and *4*, beginning with MASTERS (1901) report of *A. insignis* CARR. *(A. pinsapo × nordmanniana). Figure 1*, previously referred to, shows all the natural crosses with parent species divided into geographical regions.

Artificial Interspecific Hybrids:

In 1926, JACKSON and DALLIMORE stated that, "most hybrid conifers, which appear to be commonest in the genus *Abies*, have been artificially produced."

JOHNSON (1939) lists three fir hybrids, one natural and two artificial. SMITH and NICHOLS (1941) also refer to three fir hybrids, two naturally occurring and one artificially produced. It appears that they are referring to the same crosses reported by JOHNSON. These authors were unable to confirm the reports, by several authors, of the artificial cross *A. cephalonica × pinsapo*.

By 1941 there had been eight artificial fir hybrids produced; however, all were not reported until 1949. *Table 3* is a chronological compilation of the confirmed artificial hybrids produced as of 1962.

In the United States, JACKSON DAWSON successfully crossed *A. nordmanniana* with both *A. cilicica* and *A. cepha-*

Table 2. — Natural Arboretum or Plantation Interspecific *Abies* Hybrids. —

The following crosses have originated from seed collected in arboreta, gardens, and plantations. The first listed species is the female parent except where[1]) follows the cross; these crosses[1]) may have the male and female parents interchanged.

Cross	Date, Country of Origin; Date Reported	References
1. *A. pinsapo × nordmanniana (A. insignis* CARR.)	1872, Fr.; 1901	40, 29, 8, 51, 4
2. *A. balsamea × sibirica* and Reciprocal	Russia; 1901	3, 44
3. *A. pindrow × spectabilis*[1])	Eng.; 1909, 31	11, 2, 51
4. *A. pindrow × pinsapo (A. vasconcellosiana* FRANCO)	Portugal; 1946	16, 17, 45
5. *A. pinsapo × numidica (A. pinsapo vel hybrida)*	1912, Eng.; 1955	63
6. *A. fraseri × veitchii*	1924, Den.; 1962	*)
7. *A. nordmanniana × alba*	1924, Den.; 1962	*)
8. *A. pisapo × alba*	1924, Den.; 1962	*)
9. *A. pinsapo × nordmanniana*	1924, Den.; 1962	*)
10. *A. alba × pinsapo*[1]) *(A. pardei* GAUSSEN)	Fr., Sp.; 1937, 62	15**)
11. *A. concolor × grandis*	1951, Ger.; 1956	59, 20

*) HOLST, M. J. Personal communication (1/17/62), Petawawa For. Exp. Sta., Chalk River, Ontario, Canada.

**) RAMOS, J. L. Personal communication (1/29/62), Escuela Tenica Superior de Ing. de Montes, Madrid, Spain.

All species names according to REHDER, 1958.

Table 3. — Confirmed Artificial Interspecific *Abies* Hybrids produced by Controlled Pollinations. —

In the following crosses, the female parent is listed first in each case.

Cross	Date, Country of Origin; Date Reported	References
1. *A. pinsapo × cephalonica (A. vilmorinii* MAST.)	1867, Fr.; 1901	40, 29, 8 51, 11
2. *A. nordmanniana × pinsapo (A. nordmanniana speciosa* BAILLY)	1871, Fr.; 1901	40, 8, 4
3. *A. pinsapo × nordmanniana* (MOSER'S hybrids)	1878, Eng.; 1901	40, 11
4. *A. nordmanniana × cephalonica*	? 1915, U.S.; 1949	23
5. *A. nordmanniana × cilicica*	? 1915, U.S.; 1949	23
6. *A. concolor lowiana × grandis*	1924, Den.; 1934	35, 29
7. *A. sibirica × veitchii*	1941, Swed.; 1943	10
8. *A. sibirica × veitchii olivacea*	1941, Swed.; 1943	10
9. *A. sachalinensis mayriana × homolepis*	Japan; 1951	27
10. *A. koreana × veitchii*	?1952, Den.; 1960	37
11. *A. concolor × alba*	1951, Ger.; 1961	54
12. *A. concolor × amabilis*	1951, Ger.; 1961	54
13. *A. concolor × grandis*	1951, 58, Ger.; 1961	54
14. *A. concolor × nordmanniana*	1950, 51, 58, Ger.; 1961	54
15. *A. concolor × nobilis*	1950, 51, 58, Ger.; 1961	54
16. *A. concolor × sibirica*	1951, Ger.; 1961	54
17. *A. concolor × veitchii*	1950, 51, 58 Ger.; 1961	54
18. *A. alba × concolor*	1958, Ger.; 1961	54
19. *A. alba × grandis*	1958, Ger.; 1961	54
20. *A. alba × nordmanniana*	1958, Ger.; 1961	54
21. *A. alba × veitchii*	1950, 51, 58, Ger.; 1961	54
22. *A. grandis × alba*	1951, Ger.; 1961	54
23. *A. grandis × concolor*	1951, Ger.; 1961	54
24. *A. grandis × nordmanniana*	1951, Ger.; 1961	54
25. *A. grandis × veitchii*	1951, 58, Ger.; 1961	54
26. *A. homolepis × alba*	1958, Ger.; 1961	54
27. *A. homolepis × concolor*	1950. Ger.; 1961	54
28. *A. homolepis × grandis*	1958, Ger.; 1961	54
29. *A. nordmanniana × concolor*	1951, 58, 60, Ger.; 1961	54
30. *A. nordmanniana × alba*	1951, 58, 60, Ger.; 1961	54
31. *A. nordmanniana × grandis*	1951, 58, Ger.; 1961	54
32. *A. nordmanniana × veitchii*	1950, 51, 58, 60, Ger.; 1961	54
33. *A. numidica × alba*	1955, Ger.; 1961	54
34. *A. veitchii × alba*	1950, 51, 55, Ger.; 1961	54
35. *A. veitchii × concolor*	1951, Ger.; 1961	54
36. *A. veitchii × grandis*	1951, 55, Ger.; 1961	54
37. *A. veitchii × nordmanniana*	1951, 60, Ger.; 1961	54
38. *A. balsamea × lasiocarpa*	1956, Can.; 1962	*)
39. *A. fraseri × balsamea*	1956, Can.; 1962	*)

*) HOLST, M. J. Personal communication (1/17/62), Petawawa For. Exp. Station, Chalk River, Ontario, Canada. —

All species names according to REHDER, 1958.

Table 4. — Putative Artificial Interspecific *Abies* Hybrids Produced by Controlled Pollinations. —

The following crosses have not been fully evaluated for hybridity; the female parent is listed first in each case.

Cross	Date, Country of Origin; Date Reported	References
1. *A. balsamea* × *homolepis*	1960, Canada	*)
2. *A. balsamea* × *concolor*	1960, Canada	*)
3. *A. balsamea* × *nordmanniana*	1960, Canada	*)
4. *A. sachalinensis* × *recurvata*	1960, U.S.; 1961	31
5. *A. sachalinensis* × *cephalonica*	1960, U.S.; 1961	31
6. *A. sachalinensis* × *(nord.* × *ceph.)*	1960, U.S.; 1961	31
7. *A. sachalinensis* × *alba*	1960, U.S.; 1961	31
8. *A. veitchii* × *(nord.* × *ceph.)*	1960, U.S.; 1961	31
9. *A. homolepis* × *(nord.* × *ceph.)*	1960, U.S.; 1961	31
10. *A. homolepis* × *(nord.* × *cilic.)*	1960, U.S.; 1961	31
11. *A. nobilis glauca* × *recurvata*	1960, U.S.; 1961	31
12. *A. (nord.* × *ceph.)* × *(nord.* × *cilic.)*	1960, U.S.	**)
13. *A. (nord.* × *ceph.)* × *sachalinensis*	1960, U.S.	**)
14. *A. (nord.* × *ceph.)* × *homolepis*	1960, U.S.	**)
15. *(nord.* × *ceph.)* × *concolor*	1960, U.S.	**)

*) Chiasson, L. P. Personal communication (1/18/62), St. Francis Xavier University, Antigonish, N. S., Canada. —

**) Unpublished master's thesis by junior author "Interspecific Hybridization in the Genus Abies", State University College of Forestry, Syracuse, N. Y., 1962. —

All species names according to Rehder, 1958.

lonica at the Wellesley estate in Massachusetts. He accomplished these crosses before his death in 1916, although the exact year could not be found by these authors. Smith and Nichols (1941) report attempts at artificial hybridization between 1937 and 1939, but list no results. Wright (1953) also attempted crosses in 1947 and 1948 without conclusive results.

Holst, at Chalk River, Canada, successfully crossed *A. balsamea* × *lasiocarpa*, and *A. fraseri* × *balsamea* in 1956. In Nova Scotia, Chiasson (1960) was successful in obtaining seedlings from crosses with *A. balsamea* as the female parent and *A. cephalonica, grandis, homolepis, homolepis umbellata, nobilis glauca,* and *veitchii* as the male parents. All of the seedlings, however, were destroyed as a result of a fire which broke the greenhouse glass and exposed them to freezing winter temperatures. More recent attempts by Chiasson (1962)[8]) have resulted in putative fir hybrids with *A. balsamea* as the female parent and *A. homolepis, concolor,* and *nordmanniana* as the male parents.

In Europe, Larsen (1934) successfully crossed *A. concolor lowiana* × *grandis* in 1924. In 1941, Eklund (1943) crossed *A. sibirica* × *veitchii* and *A. sibirica* × *veitchii olivacea* successfully. Rohmeder's many successful crosses between 1950 and 1960 are listed in *Table 3.*

Those hybrids produced by Chiasson (1962) and those produced in the experimental part of this research are considered only as putative hybrids until further evaluation can be made *(Table 4).*

Materials and Methods

The aritificial hybridization work reported in this study was conducted at Highland and Durand-Eastman Parks in the city of Rochester, New York, and near the village of Indian Lake in the Adirondack Mountains, New York. On the basis of a flower survey conducted during the winter of 1960, 13 species and species hybrids were chosen at Rochester and five specimens of *A. balsamea* were selected near Indian Lake.

Choice of crosses attempted was limited in some specimen by existing female strobili. On other specimens with unlimited number of female strobili, all possible combinations were attempted. A bagged unpollinated control was left on each tree. On trees where the number of female strobili was abundant, self-pollinations were also attempted.

[8]) Chiasson, L. P.: Personal communication (1/18/62), St. Francis Xavier University, Antigonish, N. S., Canada.

Table 5. — Dates and Data Relative to Female Parents Involved in 1960 Hybridization. —

	sachalinensis 7	*recurvata 738*	*veitchii 13*	*nordmanniana 66*	*cilicica 123*	*cephalonica 762*	*homolepis 1*	*concolor 445 A*	*nobilis glauca 837*	*nord. × ceph. 734*	*nord. × cilic. 725*	*balsamea 1*	*balsamea 2*	*balsamea 3*	*balsamea 4*	*balsamea 5*
Isolation of female strobili	4/29	5/3	4/22 5/1	5/2	5/2	4/24 5/3	4/20 5/1	4/28	4/29	5/4	5/10	5/15	5/15	5/15	5/15	5/15
Removal of isolation	5/19	5/19	5/21	*)	(2) 5/25	5/24	5/21	5/25	5/28	5/24	5/24	5/25	5/25	5/25	5/25	5/25
Cone collection	(3) 9/11	9/11	9/10	—	—	9/11	9/10	9/10	9/11	9/11	(4) 9/11	(5) 9/15	9/15	9/15	9/15	9/15
No. strobili pollinated (1)	23	14	66	26	10	29	51	22	9	22	3	26	40	6	2	19
No. cones collected	21	14	6	0	0	29	27	19	9	22	3	25	36	2	2	19

*) All crosses destroyed (5/21) by children before isolation material removed; some crosses also destroyed on *A. veitchii* and *homolepis* female parents.

(1) Exclusive of unpollinated and inbred controls.

(2) Strobili molded in isolation bags; cones failed to develop.

(3) Cone scales falling; approximately 1/2 of seed lost

(4) Cones misformed; not developed as well as open-pollinated cones.

(5) All *A. balsamea* females — cone scales falling, approximately 1/3 of seed lost.

Pollen colection was done between April 25 and May 5, from severed branches growing in water containers in separate rooms. The collected pollen was placed in vials and stored in a refrigerated desiccator until use.

Isolation of female strobili was accomplished between April 29 and May 10 at Rochester; on May 15 on the *A. balsamea* specimens at Indian Lake. The *A. balsamea* isolation was too late (see later). Various isolation materials were used, most of them being a combination of polyethelene and parchment paper bags. *Table 5* presents the dates and data relative to the female parents involved in the hybridization program.

Artificial pollination was effected on all trees between May 10 and May 21, 1960. The dates of receptivity overlapped in some species and were quite apart in others. The pollen was applied to the female strobili, when, by visual inspection, it was thought that they were most receptive. The actual pollinations were accomplished by making a small cut into the bag with a sharp knife and by applying the pollen through the hole with the help of a camel hair brush. The hole was sealed thereafter with masking tape.

Isolation material was removed when the scales on the strobili were closed. The dates varied from May 19 to May 28.

Most of the strobili were found to have developed normally. Only in a few instances where aluminum "ice cream" type isolation material was used did some strobili show signs of molding.

Cones resulting from cross-pollination were collected on September 10—11. Cones of certain species could have been collected earlier. Some scales had already fallen from these species and about 30 per cent of the seed lost. Thirty-one crosses on three trees were destroyed by children climbing the trees of the Rochester Arboretum. All crosses on the *A. nordmanniana* specimen were destroyed.

Little information could be found with regard to seed stratification periods and temperature for exotic fir species used in the experiment. WRIGHT (1953) suggests four months' stratification based on work with four exotic fir species, *A. veitchii, A. homolepis, A. nordmanniana,* and *A. cephalonica appolinis.* With the exception of *A. concolor,* seeds from all other species were stratified for 45 days at 38° F (5° C). It was decided to stratify seeds from *A. concolor* for 15 days, after a small scale experiment showed that open-pollinated seeds began to germinate after that

female parent \ male parent	sachalinensis #7	recurvata #738	veitchii #13	nordmanniana #66	cilicica #123	cephalonica #762	homolepis #1	concolor #445A	nord. x ceph. #734	alba #408	lasiocarpa #826 arizonica	nord. x cilic. #725	balsamea #1(Pack)
sachalinensis #7		1				2			3	2		X	X
recurvata #738							X		X	X		X	
veitchii #13	- - - destroyed by children - - -								5				
nordmanniana #66	- - - destroyed by children - - -												
cilicica #123								X	X	X	X		
cephalonica #762													
homolepis #1	- - - destroyed by children - - -							1				1	
concolor #445A				X		X		2*					
nobilis glauca #837		36				X			X			X	
nord. x ceph. #734	15	X			2		46	12	3*			2	
nord. x cilicica #725	X	X	X			X	X	X		X	X	X	X
balsamea #1 (Ind. Lake)	X	X	80			X	X		X	X	49	11	X
balsamea #2 (" ")	13	10	9		4	1	2	3	X	30	X	X	X
balsamea #3 (" ")	X	X			X		X		X	X	X	X	X
balsamea #4 (" ")	X	X	35	X	X	X	X	X	X	X	X	X	X
balsamea #5 (" ")	X	50	84	X	55	X	49		X	X	X	X	X

Figure 3, 1960 Abies Hybridization, Highland and Durand-Eastman Parks, Rochester, and Indian Lake, N. Y.

4 = successful cross & # seedlings obtained; 7 = incomplete isolation & # seedlings obtained; = unsuccessful cross; X = cross not attempted; 2* = inbred seedlings

period. The seeds of each cross, having a special seed lot number for nursery purposes, were planted on May 21, 1961 and the germination results recorded at three different dates.

Experimental Results

Hybridization Results:

Cones were collected from 79 of the 137 crosses attempted. Seedlings from 27 of the crosses have survived the first growing season and the following winter. *Figure 3* is the schedule of crosses for this experiment, showing the crosses attempted and the number of seedlings obtained. Five female and eight male parent species and hybrids are represented in the successful crosses.

Only 12 of the crosses are being considered as putative hybrids at this time. Fifteen crosses, all involving *A. balsamea* as female parent, produced seedlings from the unpollinated controls.

Germination Pattern:

Table 6 shows the pattern of germination observed in the nursery seedbeds during summer 1961. This table includes only those crosses under consideration as putative hybrids.

Table 6. — Germination Pattern of Putative Hybrid Seed (All seeds planted 5/21/61). —

Seed Lot Number	Cross	No. Seeds Planted	No. Seeds Germ. As of 6/14	7/8	11/19	Germ. Per Cent
H 1—1	*A. sachalinensis* × *recurvata*	103	0	1	1	1.0
H 1—5	*A. sachalinensis* × *cephalonica*	126	0	2	2	1.6
H 1—8	*A. sachalinensis* × *(nord.* × *ceph.)*	87	2	3	3	3.4
H 1—9	*A. sachalinensis* × *alba*	73	0	2	2	2.7
H 3—2	*A. veitchii* × *(nord.* × *ceph.)*	1042	0	5	5	0.5
H 5—5	*A. homolepis* × *(nord.* × *ceph.)*	815	0	1	1	0.1
H 5—8	*A. homolepis* × *(nord.* × *cilicica)*	961	0	1	1	0.1
H 7—1	*A. nobilis glauca* × *recurvata*	422	17	36	35*)	8.3
H 8—7	*A.(nord.* × *ceph.)* × *(nord.* × *cilicica)*	70	0	2	2	2.8
The isolation material was damaged on the following crosses, and the strobili were exposed during a critical period (pollen flying or receptive strobili).						
H 8—1	*A. (nord.* × *ceph.)* × *sachalinensis*	322	9	15	15	4.7
H 8—4	*A. (nord.* × *ceph.)* × *homolepis*	1153	21	46	46	4.0
H 8—5	*A. (nord.* × *ceph.)* × *concolor*	152	0	12	12	7.9

*) one seedling died from unknown causes.

All unpollinated controls of the above crosses produced no seedlings.

The female parent is listed first and the male parent second in the above crosses.

Table 7. — Germination Pattern of Seed Involving *A. balsamea* as the Female Parent in a Cross (All seeds planted 5/21/61).

Seed Lot Number	Cross	No. Seeds Planted	No. Seeds Germinat. As of 6/14	7/8	11/19	Germ. Per cent
H 9—1	*A. balsamea 1* × *veitchii*	332	0	15	80+ *)	24.1
H 9—2	*A. balsamea 1* × *lasiocarpa arizonica*	203	4	50	55+	27.1
H 9—3	*A. balsamea 1* × *(nord.* × *cilicica)*	140	0	11	11	7.9
H 9—5	*A. balsamea 1* open pollinated	210	0	10	17	8 1
H 9—6	*A. balsamea 1* unpollinated control	45	0	1	1	2.2
H 10—1	*A. balsamea 2* × *sachalinensis*	173	0	4	13	7.5
H 10—2	*A. balsamea 2* × *recurvata*	390	1	5	10	2.6
H 10—3	*A. balsamea 2* × *veitchii*	24	0	9	9	37.5
H 10—5	*A. balsamea 2* × *cilicica*	631	0	3	4	0.6
H 10—6	*A. balsamea 2* × *cephalonica*	44	0	1	1	2.3
H 10—7	*A. balsamea 2* × *homolepis*	102	0	0	1	1.0
H 10—8	*A. balsamea 2* × *concolor*	55	0	3	3	5.4
H 10—10	*A. balsamea 2* unpollinated control	212	2	26	55	25.9
H 11—1	*A. balsamea 4* × *veitchii***)	205	0	19	35	17.1
H 12—1	*A. balsamea 5* ×*recurvata*	87	9	40	50+	57.5
H 12—2	*A. balsamea 5* × *veitchii*	428	4	80	80+	18.7
H 12—3	*A. balsamea 5* × *cilicica*	94	8	52	55	58.5
H 12—4	*A. balsamea 5* × *homolepis*	103	7	45	49	47.6
H 12—5	*A. balsamea 5 open-pollinated*	308	9	82	82+	26.6
H 12—6	*A. balsamea 5 unpollinated control*	410	0	41	41+	10.0

*) Final seedling count estimated since erratic germination caused some seedlings to be later; seed coats attached to cotyledons, survival through winter doubtful.

**) Only cross attempted on *A. balsamea* 4.

All unpollinated controls on the female parent trees involved in these crosses produced no seedlings.

Table 7 shows the germination pattern for those crosses involving *A. balsamea* as female parent. These crosses, as pointed out, are not under consideration for hybridity at this time. At the time this paper was written, however, some seedlings showed differences from others in the same lot, in height growth as well as in needle characteristics which might indicate that they are of hybrid nature.*)

Germination Results:

The low germination percentages recorded for those crosses under consideration as putative hybrids *(Table 6)* are evident. Eklund (1943) and Chiasson (1962)[9]) have both reported similar low germination percentages for seeds resulting from artificial interspecific hybridization attempts in the genus *Abies.*

The germination percentages for seeds involving *A. balsamea* as the female parent *(Table 7)* are relatively higher than those under consideration as putative hybrids *(Table 6).* A single native species is involved here, however, and may be responsible for part of this difference.

Only two of the attempts at producing inbred fir material by self-pollinations were successful: two seeds of *A. concolor* out of 234 seeds germinated (0.8%), and three seeds of *A. (nord.* × *ceph.)* out of 65 seeds germinated (4.6%).

It should be noted in *Table 7* that in cases where open-pollinated seeds of *A. balsamea* were sown, the germination percentages were lower than all but one of those for seeds obtained from attempted crosses. The application of additional pollen may be responsible for a higher number of filled seeds and the increase in germination. If this is the case, some of the resulting seedlings may prove to be interspecific hybrids.

Evaluation of Putative Hybrids

The seedlings resulting from these controlled pollinations can only be considered at this time as putative hybrids. Evaluation of differences between the suspected hybrids and the open-pollinated now one-and-a-half year old progenies of any one parent tree is difficult and may lead to false conclusions.

Standards set for hybridity at the Northeastern Forest Experiment Station and at the Institute of Forest Genetics in California require: (1) repetition of a cross in two or three different years, (2) planting the suspected hybrids in replicated nursery tests until such time as, (3) there are statistically significant differences between the hybrid progeny and non-hybrid progeny from the same female parent. By such standards, this experimental hybridization is the first step in a series towards the production of certified hybrids.

The attempt to use needles of hybrid seedlings imbedded in n-butyl methacrolate for cross sectioning was abandoned after literature study regarding the anatomical variability and diagnostic value of needle characters. Flous (1937) used needle characters to diagnose hybrid fir progeny, but worked with large samples of secondary needles from older trees. Masters (1889) and others are of the opinion that needles which immediately follow the cotyledons differ in form, attachment, arrangement, and even in structure from those which characterize the adult tree.

To obtain however, some preliminary, more general, figures on the performance of the putative hybrids the following *Table 8* has been prepared.

Miscellaneous Observations

There are a number of different observations that have been made during the study of which the following two deserve special attention:

Relationship of Graft Flushing and Receptivity:

Scionwood from most of the species used in the experiment was greenhouse grafted at Syracuse. All rootstocks were *A. balsamea,* and grafts were made on 2/3/60. The dates of bud flushing on the grafted scions were recorded in an attempt to relate this flushing with the receptivity of female strobili observed later on the same species. Grafts of *A. veitchii,* and *A. sachalinensis* flushed first, fol-

*) All crosses were repeated in spring 1962 and new combinations with *A. balsamea* as female parent incorporated.

[9]) Personal communication cited.

Table 8. — Seedling Measurements After 6th and 13th Month — (Average height included measurements to top of terminal bud).

Seed Lot	Cross	Live Seedlings		Ave. Ht. (mm)	Ave. Needle Length (mm)	Ave. Ht. (mm)	Ave. Needle Length (mm)
		1961	1962	11/2/61		6/18/62	
	A. sachalinensis o. p.*)	101	100	19	9	39	12
H 1—1	*A. sachalinensis* × *recurvata*	1	1	23	12	63	19
H 1—5	*A. sachalinensis* × *cephalonica*	2	1	23	9	53	13
H 1—8	*A. sachalinensis* × *(nord. × ceph.)*	3	3	21	9	60	16
H 1—9	*A. sachalinensis* × *alba*	2	1	21	8	50	13
	A. veitchii o. p.	32	32	20	7	46	11
H 3—2	*A. veitchii* × *(nord. × ceph.)*	5	5	20	7	58	14
	A. cephalonica o. p.	74	74	33	11	68	14**)
H 5—5	*A. homolepis* × *(nord. × ceph.)*	1	1	27	12	75	17
H 5—8	*A. homolepis* × *(nord. × cilicica)*	1	1	18	12	52	14
	A. nordmanniana × *cilicica* o. p.	2	2	24	11	76	19
	A. concolor o. p.	—	253	—	—	158	38**)
	A. concolor selfed	2	2	—	—	76	32**)
H 7—1	*A. nobilis glauca* × *recurvata*	35	35	37	15	92	21**)
	A. nobilis glauca o. p.	6	4	30	6	62	13
	A. nordmanniana × *cephalonica* o. p.	2	2	33	10	45	13
H 8—1+)	*A. (nord. × ceph.)* × *sach.*	15	15	—	—	86	18**)
H 8—4+)	*A. (nord. × ceph.)* × *homolepis*	46	46	—	—	85	20**)
H 8—5+)	*A. (nord. × ceph.)* × *concolor*	12	12	—	—	64	17**)
H 8—7	*A. (nord. × ceph.)* × *(nord. × cil.)*	2	2	22	13	28	16***)
	A. nord. × ceph. selfed	3	3	—	—	63	17**)

*) o. p. = open pollinated.
**) Some seedling showed second flush in year.
***) Seedlings just beginning second growing season.
— not measured in fall 1961.
+) The isolation material was damaged on the crosses (see *Table 6*).

lowed by *A. recurvata* and *A. lasiocarpa arizonica*. Other grafted species did not flush until two weeks later.

Of the parent trees, *A. sachalinensis, A. veitchii, A. recurvata,* and *A. cephalonica* were the first to develop receptive strobili. The specimen of *A. lasiocarpa arizonica* produced no female strobili in the spring of 1960.

Early graft flushing and early strobili receptivity seemed to be related in at least some of the species used in the experiment. If such a relationship could be proven, it would be invaluable in interspecific hybridization attempts involving a large number of species. Perhaps cuttings could be used as well as grafts to predict receptivity periods. Similar studies involving ecotypes of the same species would be of value in work with intraspecific hybridization, especially in the case of seed orchards.

Determination of Viable Seed:

In cleaning the seed sources with the "South Dakota Seed Blower", it was noticed that a large number seemed to be light and empty. A few X-ray pictures were taken of sample seed lots and showed that only about 3% of the seed, on the average, had fully formed embryos and endosperm. "Pinch" tests of soaked seeds after stratification, as described by Wright (1953), indicated that 5% of the seeds were full. The average germination percentage of seeds under consideration as putative hybrids was 3.1%. The differences reflect the relative refinements of the two tests. The few X-rays revealed many stages between empty seeds and seeds with a fully developed embryo and endosperm.

Discussion

Geographical Distribution and Crossability:

The summary of reported crosses *(Figure 1)* shows the species crosses reported in the genus *Abies*. The species listed are divided into three geographical regions of the world: Mediterranean (including European), Asian (including Siberian), and North American. It is apparent from the figure that species from different geographical regions cross readily, as in other conifers and hardwoods. This suggests that the species may be closely related and may account in part for the unsuccessful attempts made at dividing the genus into sections.

The figure includes only those species which have been reported as being involved in natural or artificial crosses. The Asian species appear to be most neglected in studies and experimental hybridization attempts. Part of this neglect may be due to the lack of Asian species in areas where studies are being conducted.

In the Mediterranean region, the species are especially prone to hybridize. *A. borisii-regis, A. equi-trojani, A. bornmülleriana,* and *A. nebrodensis* all appear to be of hybrid origin. Pavari (1941) believes that *A. nordmanniana, A. bornmülleriana,* and *A. equi-trojani* are very closely related and have been separated in relatively recent times. *A. borisii-regis* occurs in an area where *A. cephalonica* and *A. alba* have overlapping ranges and has many characters intermediate between these species.

Sargent (1898) regards the Cascade Range in Oregon as the "headquarters" of the genus *Abies,* with six species along the 160 mile north-south range. *A. nobilis* and *A. grandis* of the north are replaced by *A. magnifica* and *A. concolor,* respectively, in the south. *A. lasiocarpa* and *A. amabilis* extend the full length of the north-south range. Sympatric species combinations include: *A. magnifica* and *A. concolor; A. lasiocarpa, A. amabilis,* and *A. nobilis; A. concolor, A. lasiocarpa,* and *A. grandis;* and *A. amabilis* and *A. grandis* (Sargent, 1898; Harlow, 1958).

The cross *A. concolor* × *grandis* has occurred naturally in a German arboretum and has also been produced artificially. It has not been reported as occurring naturally where these species overlap in ranges.

On the islands of Japan, *A. mariesii, A. veitchii,* and *A. homolepis* have overlapping ranges. To the best of the authors' knowledge, however, none of these species have been reported as having crossed naturally or as having been crossed artificially. *A. sachalinensis mayriana* × *homolepis* has been reported as being artificially produced.

The only report of a cross between Chinese species found in the literature was *A. sibirica* × *nephrolepis*. a natural cross occurring in northeastern Heilungkiang Province (TAKENOUCHI and CHIEN, 1957).

Evolution of Species

A study of the evolution and phylogeny of fir species is not within the scope of this research. It would require a more complete study of the morphology, distribution, genetic data, and perhaps fossil history of the genus. It may be of interest, however, to mention studies which have been completed in relation to the evolution of fir species.

Certain histological regions of fir needles have received special study in attempts to discover their function and phylogenetic importance. FULLING (1934) presents a review of the literature concerning these studies. According to GAUSSEN (1937), the firs show a trend in the anatomical character of the resin canals of needles. Resin canals are median or centrally located in primitive types and marginal in evolved types. In *A. pinsapo*, a primitive fir, needles on sterile branches of young trees have marginal canals; needles on sterile branches of old or adult trees and on fertile branches have median canals. Only the youthful needles have the evolved type, i. e., with marginal canals. In *A. alba*, a more evolved fir, marginal canals are present in needles of both the young and old sterile branches, with median canals being present on fertile branches. Here the youth form is not differentiated from the adult sterile parts. Finally in *A. bracteata*, the most evolved fir according to GAUSSEN, the evolution proceeds to transform fertile needles, as well, to a condition with marginal canals. All the needles have marginal canals. The character evolution is complete; the needle character (resin canal placement) of the young tree does not suggest any trends.

FLOUS (1936) suggests that the needle characters of fertile twigs are more primitive than those of sterile twigs, and that characters of young sterile twigs are more evolved than those of older sterile twigs. This view is supported by GAUSSEN's example in firs. GAUSSEN though, gives no explanation of why marginal canals should be considered more evolved than median canals.

If GAUSSEN's theory is correct, and resin canal placement is an indicator of the primitiveness of firs, one could speculate about the species type from which other firs evolved in a geographic region.

In the Mediterranean region, *A. numidica* and *A. pinsapo* with median resin canals, would be the forerunners of other fir species in the region. Using this same criterion, however, *A. borisii-regis*, which is considered to be of hybrid origin between *A. cephalonica* and *A. alba*, with median canals is more primitive than its supposed parents. Instead of being of hybrid origin, it may have been a source for the production of the species *alba* to the north and *cephalonica* to the south. TURRILL (1937) suggests such a possibility.

In eastern North America, *A. balsamea* and *A. fraseri* both have median resin canals and would be considered primitive species. *A. lasiocarpa* and variety *arizonica* with median canals would be the most primitive species of fir in western North America.

Most of the species of Japan and western China have median resin canals. Exceptions are *A. recurvata* and *A. chensiensis* of China with marginal canals, and *A. koreana* and *A. mariesii* of Korea and Japan, respectively, with sub-marginal canals. Asia then would contain the bulk of primitive fir species and perhaps should be considered the prime source of other fir species. *A. sibirica* with median canals would be considered primitive and, being similar to *A. balsamea* in this and other respects, may have developed from similar sources.

Transmission of Characters to Hybrids:

FLOUS (1937) investigated the possibility of the hybrid origin of *A. pardei* and *A. borisii-regis* based on the transmission of parental characters. A known artificial hybrid, *A.* × *vilmorini*, was first studied along with *Larix eurolepis (L. decidua* × *leptolepis)* to determine different character transmission. It was found that qualitative characters, i. e., disposition of needle resin canals, cross-sectional needle form, anatomical pecularities of branches, form of cone bract, etc., in the hybrids were like those found in either of the parents. Quantitative characters, i. e., needle length, number and length of stomata lines, branch pubescense, cone bract length, etc., in the hybrids were intermediate between those of the parent species.

Based on the hypothesis that parents' qualitative characters are maintained and quantitative characters are intermediate in hybrids, FLOUS concluded that *A. pardei* was probably a hybrid between *A. alba* and *A. pinsapo*. She concluded that *A. borisii-regis* seemed to be a hybrid between *A. alba* and *A. cephalonica*. It was added, however, that not enough proof was available regarding the quantitative characters of these complex hybrids (back-crosses between both putative parents exist in "hybrid swarms").

ROHMEDER (1961) has investigated the transmission of such characters as twig pubescense, resinous buds, and needle stiffness in his artificially produced hybrids. The transmission of the resinous condition of buds in the cross *A. veitchii* × *alba* was as a qualitative character as described by FLOUS. All of the hybrids had nonresinous buds as in the female parent *A. veitchii*. In other cases examined, however, the resinous bud condition was transferred as a quantitative character.

Compatibility — Incompatibility:

A large range probably exists, between complete compatibility and complete incompatibility in species crosses.

The generally accepted criterion for compatibility among tree improvement workers is that seedlings be produced from the hybrid seed. It was also mentioned that X-ray studies have shown many stages between fully empty and completely full seed. The results of these studies have shown that in many cases, fertilization has occurred (the cross is compatible by theoretical definition) but that the embryo and/or endosperm has collapsed in some process following the union of egg and sperm cells (KLAEHN and WHEELER, 1960).

It is common knowledge that plants can be obtained by excising embryos and growing them on artificial media. Many of the seeds from species crosses may have failed to produce seedlings as a result of interference in some process leading to germination. Such crosses may well be considered compatible if seedlings can be produced through excised embryo and artificial germination techniques.

Crosses between species which have produced seedlings then, can certainly be considered as being compatible. Failure to produce seedlings, however, does not necessarily indicate incompatibility.

MERGEN and LESTER (1962) have stated that, "unless the experimenter knows his material, failures in obtaining hybrid seed are as much a reflection on his methods as of

the genetic incompatibility barriers that might exist." This statement was made in support of a basic study of the microsporogenesis in several fir species.

It can be argued that studies of this and other basic problems should be complete before hybridization attempts are made in a study of compatibility. Basic studies are time consuming as compared to hybridization attempts. Hybrid material produced through artificial pollinations can provide information on species compatibility in a short period, and the material can be evaluated for possible use in forest situations.

Summary and Conclusions

Through a literature review and a letter survey study, reports of natural and artificial *Abies* hybrids were compiled into a modified crossability pattern. An attempt was made to expand this compiled pattern by attempting controlled pollinations in the spring of 1960.

Twelve female and 13 male parent species and hybrids were represented in the 137 inter-species crosses attempted on mature arboretum and forest specimens. Twelve of these crosses resulted in seedlings which are under consideration for putative hybridity. Unpollinated controls of the species represented by these crosses produced no seedlings, and it is assumed that no accidental pollinations occurred.

Fifteen additional crosses, all involving *A. balsamea* as the female parent, produced seedlings from the unpollinated controls. The crosses on these specimen are not being considered as putative hybrids at this time. It is believed that the female strobili on these trees were isolated after their period of receptivity had begun. A higher germination percentage, however, was recorded for seeds of the controlled pollinations from these trees than for seeds of the open-pollinated controls. If this difference is due to the application of the additional pollen, future evaluation of the seedlings may reveal hybrids.

Attempts at producing inbred material was successful in only two cases. Seedlings of inbred *A. concolor* and *A. (nordmanniana* × *cephalonica)* have survived two growing seasons in the nursery. Open-pollinated seedlings of all the species used in the experiment are being grown along with the putative hybrid and inbred seedlings for future evaluation.

The compiled and expanded crossability pattern resulting from this research is "modified" in the sense that: it does not show the relative success in obtaining seedlings from the crosses (seedlings/seeds/cross), and it separates the parent species into geographical regions.

It is impossible to obtain seedling germination percentages for the crosses effected by some of the earlier workers. Of the more recent workers, many have not reported such data. The pattern does show crossability within and between species of different regions, but does not indicate degree of crossability.

The summary of reported crosses in the genus *Abies* shows that species within the Mediterranean region are especially prone to hybridize. Indication is that many species crosses can be accomplished between the North American species. The lack of hybrids reported between Asian species is probably due to incomplete study or the lack of these species in parts of the world where hybridization attempts are being made. Interspecific hybrids between species of different regions have been accomplished to a greater extent in recent years.

The pattern of species crosses in the genus *Abies* suggests that many species are closely related, and that more crosses may be possible. Such a relationship also suggests that perhaps a geographic rather than a genetic or physiological separation of species has occurred as the genus evolved. Wright (1962)[10]) holds this view for fir, and Sax and Sax (1933) and Chiarugi (1959) for coniferous species in general.

There is no separation of the genus into sections, and considerable difficulty has been experienced in attempting to do so. No relationship is here suggested between taxonomically allied species and crossability.

Certain species have been suggested as being more primitive than others by Flous (1936) and Gaussen (1937). Crosses between presumed primitive and more evolved species have been reported. Further interspecific hybridization attempts may reveal information as to the taxonomic and evolutionary position of species in the genus.

Hybrid vigor has been reported for many of the species crosses in the genus *Abies*. It is important to remember that this vigor is exhibited in certain areas of the world under different environmental conditions. It may not be exhibited under certain sets of environmental conditions. Those cases of vigor and non-vigor that have been reported for fir hybrids have been compiled and are shown in a figure in the text. In most cases where F_1 fir hybrids have been compared with parent species of the same age under like conditions, some hybrid vigor has been reported.

Reference was made in the text to those fir hybrids that have been reported as being fertile — producing seeds and seedlings. The experiments conducted in this study prove the fertility of the hybrids *A. nordmanniana* × *cilicica* and *A. nordmanniana* × *cephalonica* when they are used as either the male or female parent.

A crossability pattern showing the relative crossability among species can be developed only after more complete experimentation. Reports of complete incompatibility may prove to be in error, for it is possible that fertilization may have taken place. Failure to produce seedlings may be the result of interference in some process of seed development or seed germination.

Additional experimental hybridization, conducted with some knowledge of the species and techniques specific to the genus, can contribute valuable information in regards to crossability. Successful results from such hybridization indicates crossability. Failures from such hybridization can suggest those species which may be used in studies to determine basic "floral" and fertilization peculiarities.

Zusammenfassung und Folgerungen

Mit Hilfe von Literatur und brieflicher Umfrage wurden natürliche und künstliche *Abies*-Hybriden in einem modifizierten Kreuzungschema zusammengestellt. Darüber hinaus wurde versucht, das zusammengestellte Kreuzungsschema durch kontrollierte Kreuzungen im Frühjahr 1960 zu erweitern.

Zwölf weibliche und 13 männliche Eltern-Arten und Hybriden waren an den 137 versuchten interspezifischen Kreuzungskombinationen an Arboretum's und Wald-Specimen beteiligt. Zwölf Kreuzungen erbrachten Sämlinge, die als mögliche Hybriden angesehen werden. Unpollinierte Kontrollen der fraglichen Arten ergaben keine Sämlinge, und es wird angenommen, daß keine zufälligen Einkreuzungen mit unerwünschtem Pollen erfolgte.

[10]) Personal communication cited.

Fünfzehn weitere Kreuzungen, alle an *A. balsamea* als weiblichem Elter ausgeführt, ergaben aus den unpollinierten Kontrollen Sämlinge. Es wird vermutet, daß die Isolierung der weiblichen Zapfenblüten zu einem Zeitpunkt erfolgte, als die Empfänglichkeit bereits begonnen hatte. Ein höheres Keimergebnis wurde jedoch für die kontrollierten Kreuzungen im Vergleich zu den freiabgeblühten Kontrollen festgestellt. Wenn dieser Unterschied auf die Anwendung zusätzlichen Pollens zurückzuführen ist, so dürfte eine zukünftige Auswertung der Sämlinge Hybriden erwarten lassen.

Selbstungen waren nur in zwei Fällen erfolgreich. Sämlinge von geselbsteter *A. concolor* und *A. nordmanniana* × *cephalonica* haben zwei Jahre in den Saatbeeten überlebt. Freiabgeblühtes Saatgut von allen Baumarten, die in dem Versuch verwendet wurden, wachsen gleichzeitig mit den vermutlichen Hybriden und Selbstungen für spätere Auswertung auf.

Das zusammengetragene und erweiterte Kreuzungsschema ist in der Weise „modifiziert", daß es nicht den relativen Erfolg einer Kreuzung (Sämlinge/Samen/Kreuzung) angibt und daß es die Eltern-Arten in geographische Regionen trennt.

Es war unmöglich, die Keimprozente für Kreuzungen zu erhalten, die von früheren Forschern ausgeführt wurden. Auch in neueren Arbeiten sind solche Daten nicht aufgeführt. Das Schema zeigt deshalb die allgemeine Kreuzungsfähigkeit in und zwischen Arten von verschiedenen Regionen, gibt aber keine Angaben über den Grad der Kreuzbarkeit.

Die Zusammenfassung der gemeldeten Kreuzungen in der Gattung *Abies* zeigt, daß die Arten in der Mittelmeer-Region eine besondere Kreuzungswilligkeit besitzen. Es sind auch Anzeichen vorhanden, daß interspezifische Kreuzungen zwischen nordamerikanischen Arten möglich sind. Der Mangel an anerkannten Hybriden innerhalb der asiatischen Arten ist vermutlich auf die Schwierigkeit der Ermittlung oder das Fehlen gerade dieser Arten in Teilen der Welt, wo Kreuzungsversuche ausgeführt wurden, zurückzuführen. Interspezifische Kreuzungen zwischen Arten verschiedener Regionen sind erfolgreich und in größerem Maße in den letzten Jahren ausgeführt.

Das Art-Kreuzungsschema in der Gattung *Abies* läßt weiterhin annehmen, daß viele Arten sehr eng verwandt sind und daß weitere Kreuzungen möglich sind. Solch eine Verwandtschaftlichkeit läßt auch annehmen, daß vielleicht mehr eine geographische als genetische oder physiologische Trennung der Arten wirksam war, als sich die Gattung entwickelte. Wright (1962) nimmt dies für die Tannen an und Sax und Sax (1933) und Chiarugi (1959) für die Koniferen im allgemeinen.

Die Gattung ist nicht in Sektionen eingeteilt, und erhebliche Schwierigkeiten haben sich Einteilungs-Versuchen entgegengestellt. Irgend welche möglichen Beziehungen zwischen taxonomisch nahe verwandten Arten und Kreuzbarkeit werden nicht erörtert.

Flous (1936) und Gaussen (1937) nehmen an, daß gewisse Arten primitiver sind als andere. Kreuzungen zwischen angenommenerweise primitiven und weiter entwickelten Arten sind berichtet. Weitere interspezifische Kreuzungsexperimente mögen hinsichtlich der taxonomischen und entwicklungsmäßigen Stellung von Arten in der Gattung Hinweise geben.

Heterosis wurde für viele Kreuzungskombinationen in der Gattung *Abies* berichtet. Es muß jedoch darauf hingewiesen werden, daß Heterosis in gewissen Gebieten der Erde unter unterschiedlichen Umweltbedingungen auftrat. Dies mag jedoch nicht der Fall sein, wenn andere Bedingungen gegeben sind. Die Fälle, wo Hybrid Stärke und Nicht-Stärke gemeldet wurden, wurden zusammengestellt und sind in einer Figur im Text zu finden. In den meisten Fällen, wo F_1 Tannenhybriden mit den Elternarten des gleichen Alters und unter gleichen Umweltbedingungen erwuchsen, wurde ein bestimmter Grad von Heterosis gefunden.

Im Text wird auch auf solche Tannenhybriden hingewiesen, die fertil sind, d. h. Samen und Sämlinge produzieren. Die Experimente in dieser Arbeit beweisen die Fertilität der Hybriden *A. nordmanniana* × *cilicica* und *A. nordmanniana* × *cephalonica*, wenn sie sowohl als männlicher wie auch weiblicher Elter benutzt werden.

Ein Kreuzungsschema, das die relative Kreuzbarkeit unter den Arten angibt, kann nur nach zusätzlichen Experimenten entwickelt werden. Auch muß darauf hingewiesen werden, daß Berichte von völliger Unkreuzbarkeit sich als Irrtum herausstellen können, da es möglich ist, daß Befruchtung stattgefunden hat. Das Fehlen von Sämlingen kann nämlich auch in Unterbrechung des Entwicklungsprozesses des Samens oder durch das Nichtkeimen sonst normalentwickelter Samen hervorgerufen sein.

Zusätzliche Kreuzungsexperimente, die mit guter Kenntnis der Arten und besonderen Techniquen, spezifisch für die Gattung ausgeführt werden, können wertvolle Informationen hinsichtlich Kreuzbarkeit erbringen. Erfolgreiche Kreuzungen beweisen Kreuzbarkeit. Mißerfolge von Kreuzungen mögen solche Arten erkennen lassen, die besondere Aufmerksamkeit hinsichtlich Blüten- und Befruchtungsbesonderheiten verdienen.

Résumé

Titre de l'article: *Hybridation interspécifique dans le genre Abies.*

Grâce à une revue bibliographique et à une étude par lettre-circulaire, des indications ont été réunies sur des hybrides naturels et artificiels du genre *Abies* et regroupées dans un schéma d'hybridité modifié. On a essayé de compléter ce schéma en pratiquant des pollinisations contrôlées au printemps de 1960.

12 espèces ou hybrides pris comme parent femelle et 13 pris comme parent mâle étaient représentés dans les 137 croisements interspécifiques essayés sur 1 arboretum et sur des individus en forêt. 12 de ces croisements ont donné des semis qui sont étudiés comme pouvant être des hybrides. Les témoins non contrôlés des especes représentées dans ces croisements n'ont produit aucun semis et on est certain qu'aucune pollinisation accidentelle ne s'est produite.

15 autres croisements, tous comprenant *A. balsamea* comme parent femelle ont produit des semis à partir des témoins non pollinisés. Ces croisements ne sont pas considérés maintenant comme des hybrides possibles. On pense que les fleurs femelles de ces arbres ont été isolées après le début de la période où elles sont réceptives. Cependant on a obténu un pourcentage de germination plus élevé à partir des graines venant de pollinisation contrôlée qu'à partir de celles venant de pollinisation libre. Si cette différence est due à l'application du nouveau pollen, l'examen futur des semis pourra révéler l'existence d'hybrides.

Les essais de production de matérial autofécondé n'ont réussi que dans deux cas. Des semis autofécondés d'*A.*

concolor et *A. (nordmanniana* × *cephalonica)* ont survécu deux saisons en pépinière. Des semis issus de pollinisation libre de toutes les espèces utilisées sont élevés en comparaison avec les hybrides et les semis autofécondés présumés.

Le schéma d'hybridité ainsi établi et élargi est modifié dans le sens suivant: il ne donne pas le succès des croisements par le nombre de semis obtenus rapporté au nombre de graines obtenues par croisement et il subdivise les espèces en régions géographiques.

Il est impossible de connaître les pourcentages de germination obtenus lors des croisements effectués par certains des premiers chercheurs. Même parmi les plus récents, beaucoup n'ont pas fourni ces données. Le schéma montre l'hybridité à l'intérieur et entre les espèces de différentes régions, mais il n'indique pas le degré d'hybridité.

La liste des croisements reconnus dans le genre *Abies* montre que les espèces de la région méditerranéenne s'hybrident avec une particulière facilité. Il semble que de nombreux croisements interspécifiques puissent être effectués entre les espèces d'Amérique du Nord. L'absence d'hybrides reconnus entre les espèces asiatiques est probablement due à une connaissance incomplète ou à l'absence de ces espèces dans les régions du monde où des essais d'hybridation ont été faits. Au cours des dernières années, des hybrides interspécifiques entre des espèces de différentes régions ont été réalisés sur une plus grande échelle.

La schéma des croisements interspécifiques dans le genre *Abies* suggère que beaucoup d'espèces sont proches parentes et que le nombre des croisements possibles pourrait être plu grand. Ces parentés suggèrent également que la séparation géographique a peut-être joué dans l'évolution du genre un rôle plus grand que l'isolement génétique ou physiologique. Cette idée est adoptée par WRIGHT (1962) pour les sapins, et par SAX et SAX (1933) et CHIARUGI (1959) pour les espèces de conifères en général.

La genre n'est pas séparé en sections, et les essais qui ont été faits dans ce sens se sont heurtés à des difficultés considérables. On pense ici qu'il n'existe aucune relation entre la parenté taxonomique des espèces et leur hybridité.

FLOUS (1936) et GAUSSEN (1937) pensent que certains espèces sont plus primitives que d'autres. On a signalé des croisements entre des espèces présumées primitives et d'autres plus évoluées. De nouveaux essais d'hybridation pourraient donner des indications sur la position taxonomique et évolutive des espèces dans le genre.

L'hétérosis a été signale pour de nombreux croisements interspécifiques de sapin. Il est important de rappeler que ce phénomène se manifeste dans certaines régions du monde sous des conditions écologiques différentes. Il se peut qu'il ne se manifeste pas dans certaines conditions de milieu. Les cas de présence et d'absence d'hétérosis signalés pour les hybrides de sapin ont été regroupés et sont traduits par une figure dans le texte. Dans la plupart des cas où des hybrides F_1 ont été comparés avec des espèces parentes du même âge sous des conditions analogues, on a signalé un certain hétérosis.

L'article mentionne les hybrides qui ont été signalés comme fertiles, c'est-à-dire susceptibles de produire des graines et des semis. Les expériences conduites dans cette étude prouvent la fertilité des hybrides *A. nordmanniana* × *cilicica* et *A. nordmanniana* × *cephalonica* lorsqu'ils sont employés soit comme parent mâle, soit comme parent femelle.

Un schéma d'hybridité, montrant l'hybridité relative parmi toutes les espèces, ne pourra être établi qu'après une expérimentation plus complète. Il se peut que certaines mentions d'incompatibilité complète soient erronées. La fertilisation a pu se produire, mais l'échec pour la production de semis peut être dû à certains facteurs défavorables au cours du développement de la graine ou de sa germination.

On pourra obtenir des renseignements de valeur en ce qui concerne l'hybridité par de nouvelles hybridations expérimentales menées avec une certaines connaissance des espèces et des techniques spécialement appropriées à ce genre. Le succès des résultats de ces hybridations indique l'hybridité. L'échec de ceelles-ci peut suggérer les espèces qui pourraient être employées dans des études qui auraient pour but de déterminer les particularités florales et les caractères propres de la fertilisation.

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Introgressive Hybridization between two Minnesota Birches[1])

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Introduction

Natural interspecific hybridization in the genus *Betula* is relatively common, with numerous examples on record. Some of the earliest hybrids were described by REGEL (1865), who also pointed out that since F_1 hybrids often have sterile pollen, they are more likely to be pollinated by either of the parents. He realized that such backcross progenies rather than being intermediate between the parental species, tend to resemble the recurrent parent more closely.

In spite of the many recorded instances of hybridization between members of the genus, few cases of introgression have been demonstrated. The European white birches, *Betula verrucosa* EHRH. *(B. pendula* ROTH) and *B. pubescens* EHRH. have previously been regarded as one species, *B. alba* L. Recently the similarity between these species has been interpreted as resulting from introgressive hybridization between them by YURKEVICH and GEL'TMAN (1956) in Russia, JENTYS-SZAFEROWA (1950) in Poland, STERN (1959) and NATHO (1959) in Germany. NATHO also showed that *B. humilis* SCHRANK was introgressing into *B. verrucosa* and *B. pubescens*. In the United States, FROILAND (1952) found evidence of introgression of *B. occidentalis* HOOK. *(B. fontinalis* SARG.) into *B. papyrifera* MARSH. in a hybrid swarm near Boulder, Colorado.

This paper deals with a case of introgressive hybridization between bog birch, *B. pumila* var. *glandulifera* REGEL and paper birch, *B. papyrifera* MARSH. According to the classification of the genus by WINKLER (1904), both species belong to the section *Eubetula* REGEL. *B. pumila* L., together with all the other shrubby birches, is a member of the subsection *Nanae* REGEL, while *B. papyrifera* and most other white-barked tree birches belong to the subsection *Albae* REGEL. The major distinctions between the two species are their habit and bark characteristics. *B. pumila* is

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