Hybridization of a Rocky Mountain fir (*Abies concolor*) and a Mexican fir (*Abies religiosa*)[1]

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Received September 8, 1987

Accepted January 15, 1988

ST. CLAIR, J. B., and CRITCHFIELD, W. B. 1988. Hybridization of a Rocky Mountain fir (*Abies concolor*) and a Mexican fir (*Abies religiosa*). Can. J. For. Res. **18**: 640–643.

Interspecific crosses of *Abies religiosa* (HBK.) Schlecht. & Cham. (oyamel) with *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. var. *concolor* (white fir) and *Abies magnifica* A. Murr. (California red fir) were undertaken to explore the relationships between these species. The cross with *A. magnifica* produced no germinable seed, but many sound seeds were produced from the cross with *A. concolor*. These were sown in the nursery in 1968 and outplanted in 1970. In 1983, morphological characteristics of seven putative hybrids were compared with those of the *A. concolor* seed parent, herbarium specimens of *A. religiosa*, and published descriptions of both species. In addition, monoterpene composition of the putative hybrids was compared with that of the seed parent and two unrelated *A. religiosa* trees from the same provenance as the pollen parent. Results indicate that the putative hybrids are indeed hybrids between *A. concolor* and *A. religiosa*. This finding suggests that either taxonomic sections are not separated by reproductive barriers in *Abies* (as they are in *Pinus*) or that earlier classifications should be reconsidered.

ST. CLAIR, J. B., et CRITCHFIELD, W. B. 1988. Hybridization of a Rocky Mountain fir (*Abies concolor*) and a Mexican fir (*Abies religiosa*). Can. J. For. Res. **18** : 640–643.

Des croisements interspécifiques d'*Abies religiosa* (HBK.) Schlecht. & Cham. (oyamel) avec *Abies concolor* (Gord & Glend.) Lindl. ex Hildebr. var. *concolor* (Sapin blanc) et *Abies magnifica* A. Murr. (Sapin rouge de Californie) ont été expérimentés dans le but d'éviter les relations entre ces espèces. Le croisement avec *A. magnifica* n'a produit aucune graine viable, mais plusieurs graines viables ont été produites à partir du croisement avec *A. concolor*. Ces graines ont été ensemencées en pépinière en 1968 et les semis furent extraits en 1970. En 1983, les caractéristiques morphologiques de sept hybrides putatifs ont été comparés à ceux du parent *A. concolor*, à des spécimens d'herbier d'*A. religiosa* et aux descriptions des deux espèces qu'on trouve dans la littérature. En outre, la composition en monoterpènes des hybrides putatifs a été comparée avec celle du parent et celle de deux sujets d'*A. religiosa* non liés mais de même provenance que le pollen parent. Les résultats montrent que les hybrides putatifs sont en effet des hybrides entre *A. concolor* et *A. religiosa*. Ceci laisse à penser que, ou bien les sections taxonomiques ne sont pas séparées par des cloisons affectant la reproduction chez *Abies* (comme elles le sont chez *Pinus*), ou bien les anciennes classifications devraient être revues.

[Traduit par la revue]

Introduction

The Mexican highlands are an important center of speciation for the genus *Abies*; 6 of its 39 species are found in Mexico and Guatemala (Liu 1971). Interspecific hybridization involving Mexican firs may prove valuable in elucidating evolutionary relationships and taxonomic delineations of the firs of western North America. The crosses of *Abies religiosa* (HBK.) Schlecht. & Cham. (oyamel) with *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. var. *concolor* (white fir) and *Abies magnifica* A. Murr. (California red fir) reported in this paper are the first reported crosses involving Mexican firs.

Abies religiosa is widely distributed from northern Mexico southwards to the high mountains of Guatemala (Liu 1971). It is a montane species, ranging in altitude from 2100 to 4100 m. *Abies concolor* is found throughout the mountains of the western United States and northern Mexico, ranging in altitude from 610 m in the Oregon Cascades to over 3000 m in the Rocky Mountains and Sierra Nevada. Two varieties are recognized, *A. concolor* var. *concolor* of the Rocky Mountains, and *A. concolor* var. *lowiana* of the Pacific States. The crosses reported involved *A. concolor* var. *concolor*, and, unless otherwise stated, *A. concolor* hereinafter refers to this variety. *Abies magnifica* is found between 1400 and 2700 m elevation in California and southern Oregon. Liu (1971) assigned *A. religiosa* to section *Oyamel*, *A. concolor* to section *Grandes*, and *A. magnifica* to section *Nobiles*.

Although crosses involving Mexican firs have not been attempted, hybrids involving *A. concolor* have been reported frequently (Larsen 1956; Hawley and DeHayes 1985*b*; Rohmeder 1961). In 1924, *A. concolor* var. *lowiana* was crossed with *A. grandis* in one of the first successful controlled hybridizations in the genus (Larsen 1956). In addition, natural populations with characteristics intermediate between *A. concolor* and *A. grandis* are widespread in southern and central Oregon and northwest California (Hamrick and Libby 1972). *Abies magnifica* hybridizes

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readily with *A. procera* (Silen *et al.* 1965), and intermediate natural populations are found in southern Oregon and northern California (Franklin *et al.* 1979). The ease with which these species hybridize indicates that they are recently differentiated, and they are accordingly grouped within the same sections (Liu 1971).

This paper reports the results of controlled crosses of *A. religiosa* with *A. concolor* and *A. magnifica*. The cross with *A. magnifica* produced no germinable seeds, but that with *A. concolor* produced many. Evidence is given for verification of the *A. concolor* × *A. religiosa* hybrid.

Materials and methods

Pollen from a single tree of *A. religiosa* near Paseo de Cortez, Mexico (latitude 19°06′, longitude 98°41′, elevation 3400 m), was collected in 1965 and deep frozen until crosses were done in the spring of 1967. Because of the small amount of available pollen, only two crosses were possible. One seed parent was an *A. concolor* planted in the Eddy Arboretum at the Institute of Forest Genetics (IFG) in Placerville, California; the other was an *A. magnifica* in a natural stand near Lake Tahoe, California. Control crosses were also done using pollen of the same species as the seed parent. Germinable seed from the *A. concolor* × *A. religiosa* cross were sown in the IFG nursery in 1968. (The *A. magnifica* cross produced no germinable seeds.) In 1970, five putative hybrids were outplanted at the Camino Arboretum near Camino, California, and three at the Eddy Arboretum (one of which died). These putative hybrids were evaluated at 15 years of age to verify their parentage.

Morphological characteristics and monoterpene composition of the seven putative hybrids and the *A. concolor* seed parent were compared in 1983. Morphological characteristics used for comparing the hybrids with the *A. religiosa* pollen parent were as described by Liu (1971) and as gleaned from herbarium specimens of *A. religiosa*. Monoterpene composition data were obtained (E. Zavarin, unpublished data) for two unrelated *A. religiosa* individuals, one from the same stand as the pollen parent and one from a stand about 130 km to the north.

Characteristics used in this study to distinguish between *A. concolor* and *A. religiosa* include length, width, color, and angle of needles, stomata on the upper and lower needle surfaces, and a groove on the upper needle surface. Characteristics such as crown form, bark color and texture, and twig color were not useful in this study because of the age difference between the putative hybrids and the seed parent.

All trees were first examined in the field. A branch of the current year's growth was taken from each of four sides of each tree, and needle characteristics were examined with a dissecting microscope. Length, width, and number of lines of stomata were measured on two needles from each branch, and differences in those characteristics between each putative hybrid and the seed parent were tested for statistical significance with *t*-tests. In addition, differences in needle color, needle angle, and the presence of stomata and a groove on the upper needle surface were recorded.

Monoterpene composition was determined by gas chromatographic analysis of cortical oleoresin. We collected cortical oleoresin by puncturing a blister on the main stem and pressing a vial against the blister so that the resin ran into the vial. An equal amount of pentane was then added to the resin, and the sample was refrigerated until analysis. Methods for gas chromatography were those described by Smith (1977).

Results

Crosses

The *A. magnifica* × *A. religiosa* cross produced no germinable seeds out of 45 seeds in 5 cones; the control cross using a pollen from a nearby *A. magnifica* produced 19.5 germinable seeds per cone. The *A. concolor* × *A. religiosa* cross produced 9.5 germinable seeds per cone (57 in 6 cones); the control cross using pollen from the same Rocky Mountain origin produced 22.2 germinable seeds per cone (288 in 13 cones). Crossability was assessed by comparing the number of germinable seeds per cone for the hybrid cross with that for an intraspecies cross that involved a pollen parent of the same origin. Estimated crossability between *A. concolor* and *A. religiosa* was 43%. Although this estimate of crossability is based on only a single cross, the results indicate that *A. concolor* and *A. religiosa* are not separated by strong reproductive barriers.

TABLE 1. Comparison of seven *Abies concolor* × *A. religiosa* hybrids (ACAR-1 through ACAR-8) with the *A. concolor* seed parent (AC-V6) for mean needle length, needle width, and number of lines of stomata per band

Tree No.	Needle length (mm)	p*	Needle width (mm)	p	Lines of stomata per band	p
ACAR-1	43.5	0.610	2.3	0.025	11.0	0.000
ACAR-2	37.6	0.012	2.1	0.000	9.5	0.005
ACAR-3	36.0	0.001	2.2	0.000	8.7	0.800
ACAR-4	41.1	0.130	2.4	0.100	11.2	0.000
ACAR-5	41.9	0.230	2.2	0.000	10.9	0.000
ACAR-6	38.1	0.023	1.8	0.000	9.2	0.063
ACAR-8	31.1	0.000	2.0	0.000	8.6	1.0
AC-V6	44.9	—	2.5	—	8.6	—

*p-value from t-test for H_0: μ(hybrid) = μ(seed parent).

Needle length and width

Needles of *A. religiosa* are shorter and narrower than those of *A. concolor*. Needle lengths in *A. religiosa* range from 15 to 35 mm and in *A. concolor* from 40 to 60 mm; respective ranges for needle width are 1.2 to 1.6 mm and 2.5 to 3.0 mm (Liu 1971).

Needles of the putative hybrids were both shorter and narrower than those of the seed parent (Table 1). Mean needle length of the putative hybrids ranged from 31.1 to 43.5 mm; and that of the seed parent was 44.9 mm. Needles from four of the seven putative hybrids were significantly shorter ($\alpha = 0.05$) than those of the *A. concolor* parent; needles from the other three were shorter, but the differences were not significant. Needle widths of the putative hybrids ranged from 1.8 to 2.4 mm; mean needle width of the *A. concolor* parent was 2.5 mm. Needles from six of the seven putative hybrids were significantly narrower ($\alpha = 0.05$) than those of the *A. concolor* parent; the *p*-value of the seventh was 0.10. All putative hybrids were intermediate in needle length and width between the *A. concolor* parent and the range given by Liu (1971) for *A. religiosa*.

Stomata

Abies concolor stomata appear on both needle surfaces, whereas *A. religiosa* stomata appear mainly on the lower surface, with a few in the apex of the groove on the upper surface (Liu 1971). Needles of the putative hybrids were similar to those of *A. religiosa* except that some of the stomata on the upper surface were further down the groove. The *A. concolor* parent had many stomata on both surfaces.

In both species, lines of stomata on the lower needle surface are arranged in two distinct bands. *Abies concolor* has 6 to 8 lines of stomata per band and *A. religiosa* has

TABLE 2. Percent monoterpene composition in *Abies concolor* × *A. religiosa* hybrids (ACAR-1 through ACAR-8), the *A. concolor* seed parent (AC-V6), and two *A. religiosa* individuals unrelated to the pollen parent

Tree	α-Pinene	Camphene	β-Pinene	3-Carene	Myrcene	Limonene	β-Phellandrene	Terminolene
ACAR-1	15.2	17.3	14.2	37.1	4.1	10.7	1.0	0.5
ACAR-2	8.8	13.1	17.8	35.3	2.5	15.6	3.8	3.1
ACAR-3	10.6	10.1	11.5	43.3	3.8	15.8	3.1	1.9
ACAR-4	9.2	2.2	11.8	58.1	4.0	9.9	1.8	2.9
ACAR-5	10.3	13.0	23.6	38.6	3.4	6.4	2.9	1.8
ACAR-6	10.5	12.2	10.5	39.0	2.0	22.9	1.7	1.2
ACAR-8	13.0	14.3	15.2	43.8	3.0	8.4	0.9	1.4
AC-V6	26.4	8.2	11.2	37.4	11.7	3.3	t	1.9
A. religiosa								
Sample No. 1	3.5	t	14.0	41.5	2.0	37.0	2.0	na
Sample No. 2	7.0	t	21.5	64.0	1.5	3.5	2.5	na

NOTE: t, trace amounts; na, not available.

8 to 10 (Liu 1971). The number of stomatal lines per band on needles from the putative hybrids equalled or exceeded that on needles of the *A. concolor* parent (Table 1); five of the seven putative hybrids were significantly different from that parent. Although the ranges given by Liu (1971) for this characteristic do not differ dramatically between the two species, most of the putative hybrids were within, or slightly above, the range given for the pollen parent.

Needle color

Liu (1971) described the needles of *A. concolor* as pale bluish green and glaucous on both surfaces and those of *A. religiosa* as dark shiny green on the upper surface and greyish below. This difference is related to the presence of stomata on the upper needle surface in *A. concolor*. Needles of the seed parent were pale bluish green on both surfaces; those of the putative hybrids were dark shiny green on the upper surface, and thus were similar to those of the pollen parent and distinctly different from those of the seed parent.

Needle groove

Abies religiosa needles are conspicuously grooved on the upper surface, whereas *A. concolor* needles are not (Liu 1971). All putative hybrids had median grooves on the upper needle surface, although the grooves were not as distinct as those on the needles of *A. religiosa* herbarium specimens. Although intermediate between parents in this characteristic, the putative hybrids more closely resembled the pollen parent.

Needle angle

The *A. concolor* parent and the putative hybrids differed in the angle at which median needles were attached to new branchlets. Needle angle of the seed parent varied from slightly back to slightly forward along the branchlet; needles of the putative hybrids generally pointed forward at about 45°. Liu (1971) says little about needle angle, but describes *A. religiosa* as having "median needles pointing forward" and *A. concolor* as having "some of the middle ranks above directed forward." Most needles of the *A. religiosa* herbarium specimens pointed forward, and needle angle of the putative hybrids was closer to that of the *A. religiosa* herbarium specimens than to that of the seed parent. Needle angle thus appears to differentiate the putative hybrids from the seed parent.

Monoterpene composition

Cortical oleoresin from all seven putative hybrids and the *A. concolor* parent was analyzed for monoterpene composition (Table 2), which for each monoterpene is expressed as a percentage of the total monoterpenes present. Data for the two unrelated *A. religiosa* are included for comparison. The putative hybrids different from the seed parent primarily in the percentages of α-pinene, myrcene, and limonene (Table 2), and appear to be intermediate between the *A. concolor* parent and the two unrelated *A. religiosa* individuals.

Discussion

Morphological observations and analysis of monoterpene composition indicate that the putative hybrids were indeed hybrids between *A. concolor* and *A. religiosa*. Distinct *A. religiosa* traits appeared in the hybrids, including dark green needle color, absence of stomata on the upper needle surface, and presence of a median groove. The intermediate needle length and width, number of lines of stomata per band, and monoterpene composition further support the validity of these hybrids.

The difficulty of successful intersectional crosses varies in *Abies*. Hawley and DeHayes (1985*a*) found low crossability between *A. concolor* and species from the section *Balsameae*. Mergen *et al.* (1964), however, had good success in intersectional crosses of *A. sachalensis* (section *Elate*) with *A. firma* (section *Momi*), *A. mariesii* (section *Homolepides*), and *A. lasiocarpa* (section *Balsameae*), although estimates of crossability were not given. Rohmeder (1961) reported several intersectional crosses involving *A. concolor* but provided little documentation of crossability or hybrid verification.

In contrast to the success of intersectional crosses in *Abies*, taxonomic sections in the genus *Pinus* are separated completely by reproductive barriers (Critchfield 1975). The ease with which *A. concolor* and *A. religiosa* cross indicates either that sections are not separated by strong reproductive barriers in *Abies* as in *Pinus* or that the classification of Liu (1971) should be reconsidered. However, the inability of *A. magnifica* and *A. religiosa* to cross in our single attempt suggests that these two species probably are in groups that are separated by reproductive barriers.

The ease with which *A. concolor* and *A. religiosa* crossed in this study suggests that these species are recently differentiated. Indeed, *A. concolor* is the only fir indigenous to both the United States and Mexico; geographic isolation of *A. concolor* from the Mexican firs may be relatively recent. Further study of the hybridization and geographic variation of the Mexican firs and other North American firs, particularly the southern populations of *A. concolor*, should prove valuable in elucidating the evolutionary history and taxonomic delineations within the genus *Abies*.

Acknowledgements

We wish to thank R. H. Smith for assistance in analyzing monoterpene composition by gas chromatography. Crosses were done by forestry technicians at the Institute of Forest Genetics, Placerville, California.

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Branch angle in red maple trees

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Received October 20, 1987

Accepted January 6, 1988

BOZZUTO, L. M., and WILSON, B. F. 1988. Branch angle in red maple trees. Can. J. For. Res. **18**: 643-646.

The vertical branch angle 10 cm from the base of 17 branches on 6-year-old red maple (*Acer rubrum* L.) trees increased as leaves grew out and decreased when leaves abscised, with a net increase in angle. The angle 20 cm from the base of 222 branches on five 32-year-old trees did not increase with increasing branch age. Angles of young branches varied more than 37° within each year class. Angle was significantly related to branch diameter in two of five trees. Leaf weight on the branch was significantly related to branch angle in only one of five trees. Variable amounts of tension wood formed in all branches on the young trees and in 26 of 28 branches sampled from the old trees; 22 of the 45 branches examined had tension wood on both the upper and lower side of the pith. Despite the tendency to increase the angle by bending from leaf weight, long-term increases in angle were (*i*) obscured by variability in angle within each age class and (*ii*) apparently counteracted by tension wood maintaining branches at their equilibrium position.

BOZZUTO, L. M., and WILSON, B. F. 1988. Branch angle in red maple trees. Can. J. For. Res. **18**: 643-646.

L'angle vertical d'insertion des branches à 10 cm de la base de 17 branches sur des Érables rouges (*Acer rubrum* L.) âgés de 6 ans a augmenté à mesure que les feuilles prenaient de l'expansion, puis a diminué lorsque les feuilles se détachaient, ce qui a produit une augmentation nette de l'angle. L'angle à 20 cm de la base de 222 branches sur cinq sujets âgés de 32 ans n'a pas augmenté avec l'âge des branches. Les angles des jeunes branches variaient de plus de 37° pour chaque classe d'années. L'angle était relié significativement au diamètre des branches pour deux des cinq arbres. Le poids des feuilles sur les branches était relié de façon significative à l'angle des branches pour seulement un des cinq arbres. Des quantités variables de bois de tension se sont formées dans toutes les branches des jeunes sujets et dans 26 des 28 branches échantillonnées parmi les sujets plus âgés; 22 des 45 branches examinées avaient du bois de tension sur la face supérieure et sur la face inférieure de la moelle. En dépit de la tendance à l'augmentation de l'angle par suite de la courbure provoquée par le poids des feuilles, les augmentations à long terme de l'angle ont été (*i*) cachées par la variabilité de l'angle pour une même classe d'âge et (*ii*) apparemment contrebalancées par le bois de tension qui a maintenu les branches dans leur position d'équilibre.

[Traduit par la revue]

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Printed in Canada / Imprimé au Canada