Zusammenfassung

Juniperus polycarpos kommt auf großen Flächen in hohen Gebirgslagen im Iran vor. Seine Regenerationsfähigkeit ist jedoch nur sehr gering, so daß er möglicherweise dort einmal ganz verschwindet. In der Natur produzierte Samen sind meist hohl. Bei künstlicher Bestäubung werden andererseits gesunde volle Samen erhalten. Mit solchen Methoden will man deshalb jetzt Jungpflanzen für Aufforstungszwecke anziehen.

Natural Hybridization between Pinus edulis and Pinus monophylla in the American Southwest[1])

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Introduction

Pinus monophylla TORR. & FREM. is a semi-desert pine typical of the Great Basin but extending southwards into Baja California and southeastwards across Arizona into New Mexico. Its close relative, P. edulis ENGELM., is a widespread species of the Colorado Plateau and southern Rocky Mountains. Because they produce edible nuts known as *piñones* in Spanish, they are popularly called "pinyon pines". Outlying populations of these species are sympatric in several locations. Neither species deeply penetrates the range of the other, but the long interface provides an opportunity for gene flow between them.

The possibility that these species hybridize in nature has been briefly raised by several authors. COLE[3]) compared a population of P. edulis and one of P. monophylla with putative hybrids from central Utah. He showed leaf resin canal number to be intermediate in the presumed hybrids and postulated that hybridization had occurred along a Great Basin ecotone. The trees in COLE's hybrid ecotone were initially identified by the coexistence of 2-needle fascicles and 1-needle fascicles on the same shoots. He assumed the frequencies of these fascicle types to be about equal.

CRITCHFIELD and LITTLE (1966) stated cautiously that the species "may occasionally intergrade". MIROV (1967) speculated that these pinyon pine species "possibly intercross", and urged controlled breeding experiments to settle the question. MANSFIELD-JONES[4]) studied morphological variation in pinyon pines in southwest Utah in an attempt to correlate species distribution with environmental parameters. He referred to intermediate trees as "intergrades" but did not postulate a hybrid origin for them. One feature of the intergrades was the simultaneous occurrence of 1-needle and 2-needle fascicles on the same shoots.

Two recent reports from this laboratory (LANNER 1971; LANNER and HUTCHISON 1972) have discussed the distribution of putative hybrid pinyon populations in parts of Utah, but evidence of hybridity has been deferred to this paper. The objective of this study was to define the extent of natural hybridization between P. edulis and P. monophylla.

The Study

Major emphasis has been placed on geographic variation in the frequency of monophylly, i. e. the single needles that characterize P. monophylla. These single needles had been thought to develop following the abortion of one of a pair of needle primordia (DOAK 1935), but recent work shows that only one needle primordium is formed (GABILO and MOGENSEN 1973). Because of its extreme rarity elsewhere in the approximately 100 species of Pinus, monophylly is regarded here as the result of a mutation of unique value as a genetic marker. It is assumed that this mutant form has had a single origin during the evolution of the pinyon pines.[5]) For this reason, the single-needle pines of central Arizona, long considered to be P. monophylla but recently described as a variety of P. edulis by LITTLE (1968), are included here within P. monophylla.

Single-needle fascicles are found in F, progeny of the artificial cross P. monophylla X P. edulis, produced at the Institute of Forest Genetics, Placerville, California. Sixth-year shoots of three such hybrids were kindly supplied by Dr. W. B. CRITCHFIELD. Foliage of 10 shoots had 49.7 percent 1-needle and 50.3 percent 2-needle fascicles. Sample size was small (233 fascicles), and the shoots had variable frequencies of 1-needle fascicles. By contrast, foliage from 5 wind-pollinated seedlings of each of the 2 maternal parents was purely 1-needled (571 fascicles examined); and shoots of the 3 P. edulis parents contributing to the pollen mixture had only 1 monophyllous fascicle of the 688 examined. These findings demonstrate the heritable nature of monophylly.

A second valuable leaf character is the number of leaf resin canals. This quantitative character has not been widely used in studies of natural hybridization, perhaps because closely related species usually have similar numbers of leaf resin canals. But whereas P. edulis has a very stable and low number of resin canals, P. monophylla shows

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[3]) COLE, FRANKLIN R. 1965. The pharmacognosy of Utah pinyon pines. Ph. D. Thesis, University of Utah.

[4]) MANSFIELD-JONES, G., Jr. 1967. Environmental sorting of sympatric pinyon species in southwestern Utah. Ph. D. Thesis, Duke University.

[5]) MCCORMICK and ANDRESEN (1963) reported 5 percent of 1-needle fascicles in P. cembroides ZUCC., Mexican pinyon, in the Chiricahua Mts., but no mention is made of a requirement that needles be cylindrical to avoid counting fascicles that have shed all but 1 needle. I have examined a much larger sample of Mexican pinyon fascicles from several southeastern Arizona locations without finding any bona fide 1-needle fascicles.

Table 1. — Frequency of monophylly in some 2-needled pines

Species	Tree age, years	Number of fascicles examined	Frequency of monophyllous fascicles
P. resinosa[1])	5	13,180	.0017
P. resinosa[1])	30—45	8,280	.0000
P. contorta	33	10,000	.0027
P. mugo	20	10,000	.0107

[1]) From WESTING 1964.

great variability and sometimes a much higher number. According to HARLOW (1947) for example, *P. edulis* usually has 2 resin canals while *P. monophylla* has 3—9. LITTLE (1968) found 3—16 resin canals in *P. monophylla*, and in these studies, resin canal number ranged from 1 to 17. Resin canal number has been used earlier in another study of natural hybridization involving *P. monophylla* (LANNER 1974).

Resin canals are contained entirely within the needles — they do not extend into the base of the dwarf shoot. Therefore the higher number of resin canals in a *P. monophylla* needle does not result from the diverting into one needle of resin canals that would otherwise have been distributed between two needles.

Resin canal number in *P. monophylla* is not a function of needle diameter, either within or between populations. The F_1 plants mentioned above had 2 resin canals per leaf, as did both parents.

Leaves can be sampled at any time of year, and the availability of several years' foliage permits replication in time. Other morphological differences between the two species are cone, seed and needle size (all greater in *P. monophylla*), and seed coat thickness (lesser in *P. monophylla*). Cone width has been used in this study rather than length, thus allowing rodent-damaged cones to be used.

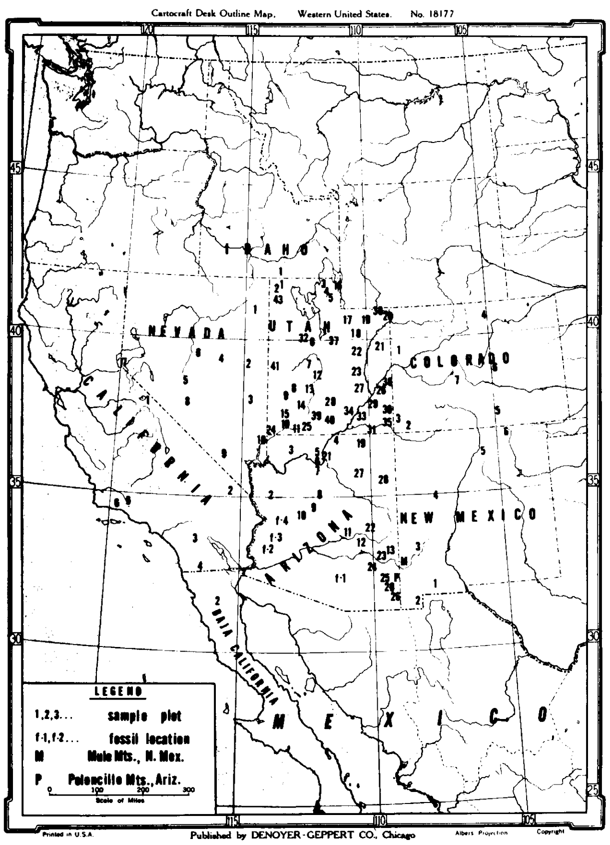

Fig. 1. — Sample plot locations in southwestern United States.

Methods and Materials

Sampling sites were located across the ranges of both species *(Fig. 1, Table 2)*. Several of these were new stations that do not appear on the most recent published maps of these species (CRITCHFIELD and LITTLE 1966; LITTLE 1971).

Table 2. — Frequency of 1-needle fascicles and leaf resin canal number in *P. monophylla* populations[1])[2])

Plot	Location	Percent 1-needle fascicles	Mean number of Resin canals per leaf
A- 2	Hualapai Mts.	99.6	3.6
A-12	Apache Mts.	98.7	3.4
A-23	Gila Mts.	99.2	4.3
A-24	Crazy Horse Pass	99.8	4.7
C- 1	Mono Lake	99.2	3.3
C- 2	New York Mts.	87.0	8.3
C- 3	Pinyon Flat	100.0	9.7
C- 4	Anza-Borrego	99.8	11.4
C- 5	Ventura	99.9	2.3
C- 6	Los Padres	100.0	2.2
I- 1	Black Pine Mts.	99.7	5.9
Mb- 2	San Matías Pass	99.9	9.0
N- 1	Wells	99.3	3.3
N- 2	Ely	99.3	3.5
N- 4	Eureka	98.5	—
N- 5	Ichthyosaur	99.6	2.7
N- 6	Austin	99.7	—
N- 7	Minden	99.2	3.9
N- 8	Tonopah	99.2	5.1
N- 9	Charleston	99.2	4.0
N-10	Virgin Mts.	100.0	6.0
U- 1	Raft River	98.8	4.4
U- 2	Rocky Pass	99.2	4.1
U-24	Shivwits	98.1	2.5
U-43	Grouse Creek Mts.	95.9	4.8

[1]) Detailed plot data will gladly be furnished by the author upon request.
[2]) A = Arizona, C = California, I = Idaho, Mb = Baja California, N = Nevada, U = Utah.

A population sample usually consisted of 5 shoots from each of 5—10 scattered trees whose crowns could be reached from the ground. Only sun leaves were taken. Most of the trees exceeded 100 years of age. A shoot usually included 2 years' growth from the leader of a first-order branch. Needle fascicles borne on these shoots were scored for needle number. Over 250,000 fascicles were examined. Because of their atypical ontogeny (LANNER 1970), summer shoots were avoided.

Resin canals were counted microscopically on free-hand sections from mid-needle. Samples usually included 10 fascicles of each of 2 years from 5—10 trees of each population. Needles of about 9,000 fascicles were examined.

Cone width was calipered to the nearest millimeter on 2—50 (mean 12.1) open mature cones from each of several populations. Vouchers from many of the sampling sites were deposited in the Intermountain Herbarium at Utah State University (UTC).

Observations

Sensitivity of Needle Number and Resin Canal Number to Environmental Conditions

Use of needle number as a criterion for detecting hybridization presupposes its relative insensitivity to environmental influences. This hypothesis was tested in a stand of *P. monophylla* in the Raft River Mountains of Utah. The population extends from the floodplain of Clear Creek (6,400 ft.) to the top of a south-facing ridge (7,700 ft.). Thus *P. monophylla* is found under an extremely varied set of conditions, unmatched in any other stand encountered during six years of field work. A "mesic" sample of 10 trees was taken on the floodplain, where the tree associates were river birch *(Betula occidentalis* Hook.), narrow-leaved cottonwood *(Populus angustifolia* James), quaking aspen *(P. tremuloides* Michx.), and Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco). An "arid" sample of 10 trees was selected 200—300 ft. above the floodplain. Associated vegetation included Utah juniper *(Juniperus osteosperma* [Torr.] Little), big sagebrush *(Artemisia tridentata* Nutt.), and prickly pear cactus *(Opuntia* sp.). Needle number in both groups averaged the same (1.01) in both 1967 and 1968 foliage. Therefore, needle number was unaffected by site differences. Resin canal number was however very significantly affected by site ($P < .001$). Thus mean resin canal numbers for 1967 and 1968 foliage combined were 3.62 on the mesic site and 5.06 on the arid site. Therefore, unusually mesic conditions can be expected to minimize, rather than exaggerate, differences in resin canal number between the pinyon pine species.

The year-to-year consistency of resin canal number was further compared by regression analysis of first-year and second-year data in 3 trees from each of 5 populations (C-4, Mb-2, N-1, N-10, U-2). Mean tree values varied from 2.2 to 13.5 resin canals per leaf. The regression of second-year resin canal number over first-year resin canal number was highly significant ($r = .95$).

It will be shown below that *P. edulis* needles almost always have 2 resin canals, so site diversity can be ruled out as a factor influencing resin canal number in that species.

Frequency of Monophylly in Other 2-needled Pines

There is the possibility of monophylly occurring due to causes unrelated to the expression of *P. monophylla* genes. Estimates were therefore made of the frequency of monophylly in three 2-needled species *(Table 1)*.

These were multi-tree samples, and the single-needled fascicles tended to be more heavily represented on some trees than on others. The single needles of *P. contorta* Dougl. and *P. mugo* Turra were superficially to deeply grooved where the flat inner surface had become infolded, thus giving the needle a nearly cylindrical shape. A small necrotic area, and occasionally a protuberance, at the base of the short shoot (under the sheath) marked the position of an aborted needle primordium. Frequency of monophylly in *P. contorta* was closely comparable to that of *P. resinosa* Ait. (Westing 1964). Mugo pine had a much higher level of monophylly *(Table 1)*.

Classification of Pinyon Pine Populations

As data accumulated, the sample populations were assigned to classes:

a. pure *P. monophylla* — a 2-year mean of at least 98 percent of the fascicles in the multi-tree sample were single-needled; and no tree had less than 90 percent single-needle fascicles in any year.
b. pure *P. edulis* — a 2-year mean of no more than 2 percent of the fascicles in the multi-tree sample were 1-needled; and no tree had more than 10 percent 1-needle fascicles in any year.
c. mixed populations — a 2-year mean of between 2 and 98 percent of 1-needle fascicles in the total population sample; or between 10 and 90 percent on any tree during any year.

These cut-off points were chosen arbitrarily to differentiate between populations that might be recently hybridized and those that may have been slightly introgressed in the past. The 2 percent of allowable monophyllous fascicles in pure *P. edulis* is about twice the frequency of monophylly found in mugo pine and is felt to provide a tolerable safety factor. Two anomalous populations are considered to be *P. monophylla* despite high frequencies of 2-needle fascicles. These will be discussed separately in detail.

Pure populations of P. monophylla

Twenty-five populations qualified as "pure" *P. monophylla* by the criteria stated above. These were from Baja California, Idaho, Nevada, Arizona, and the western corners of Utah *(Table 2)*.

Fascicles with paired needles were found in almost every population. Every population had at least 1 tree that was 100 percent 1-needled.

Resin canal number was extremely variable within plots and across the range of *P. monophylla*. The only clear geographic trend is a high resin canal value in populations forming a belt from southeastern Nevada through southern California into Baja California. The California and Baja California trees were the only ones in which mean resin canal number ever exceeded 10.

Cone width means of 10 populations averaged 64.6 mm, a value that almost exactly bisects the range 54.5—74.0 *(Table 5)*. No distinct geographic trends in cone width were detected.

Pure populations of P. edulis

Thirty-six populations from Arizona, Colorado, New Mexico and Utah had a low enough frequency of 1-needle fascicles to be classified as pure *P. edulis (Table 3)*. Some single needles were found in 29 of these populations.

Three-needle fascicles were found in every *P. edulis* stand except that from Bullfrog (U-34). A tree at Owl Canyon (Co-4) had 44 percent of its 1970 foliage and 82 percent of its 1971 needles in fascicles of 3; and similar trees were found at Hanna (U-17) and Baxter Pass (Co-1).

Fourteen of the 36 *P. edulis* populations contained one or more trees whose sampled fascicles were entirely 2-needled; and 14 populations contained one or more trees bearing all three fascicle types on combined growth of both years.

Resin canal number was remarkably uniform in the *P. edulis* stands, with only about 1.7 percent of the needles examined deviating from the normal resin canal number (2) that characterizes the species. Variation was not normally distributed. For example, of the 16 needles totally lacking resin canals, 15 were from a single tree; and this tree yielded 23 of the 39 needles with a single resin canal. Another tree contributed 30 of the 63 needles containing 3

Table 3. — Frequency of 1-needle fascicles and leaf resin canal number in *P. edulis* populations[1])[2])

Plot	Location	Percent 1-needle fascicles	Mean Number of Resin canals per leaf
A- 7	South Rim	1.0	2.0
A- 8	Oak Creek Canyon	0.0	2.0
A- 9	Jerome	0.0	2.0
A-19	Tsegi	0.1	2.0
A-20	Fort Bowie	1.5	2.0
A-21	Point Imperial	0.1	2.0
A-22	Show Low	0.7	2.0
A-27	Second Mesa	0.6	2.0
A-28	Ganado	0.2	2.0
Co- 1	Baxter Pass	0.2	2.0
Co- 2	Mesa Verde	0.3	2.0
Co- 3	Dove Creek	1.6	2.0
Co- 4	Owl Canyon	0.0	2.0
Co- 5	Walsenburg	0.0	2.0
Co- 6	Colorado Springs	0.2	2.0
Co- 7	Maysville	0.1	2.0
NM- 2	Big Hatchet Mts.	0.1	1.7
NM- 3	Mogollon Mts.	0.0	2.0
NM- 4	Acoma	0.3	2.0
NM- 5	Santa Fe	0.7	2.0
NM- 6	Cimarron	0.4	2.0
U-14	Beaver	1.4	2.0
U-17	Hanna	0.2	2.0
U-18	Indian Canyon	0.2	2.0
U-19	Yellowstone Creek	1.0	2.1
U-20	Flaming Gorge	0.4	2.0
U-22	Wellington	0.1	—
U-23	Wickiup	0.9	2.0
U-30	Monticello	0.1	—
U-31	Monument Pass	1.1	2.0
U-34	Bullfrog	0.0	2.0
U-35	Devil's Canyon	0.1	2.1
U-36	Castle Valley	0.5	2.0
U-37	Mill Fork	1.0	2.0
U-38	Sheep Creek Bay	0.0	2.0
U-40	Escalante	1.1	2.0

[1]) Detailed plot data will gladly be furnished by the author upon request.
[2]) A = Arizona, Co = Colorado, NM = New Mexico, U = Utah.

resin canals; and 15 of the remainder were from a third tree. These trees were all from different locations.

Mean cone widths of 12 populations averaged 42.5 mm *(Table 6)*. There was much variation in cone width, but no geographic trend was noted.

Mixed populations of P. monophylla and P. edulis

The 34 mixed populations are a very diverse group *(Table 4)*. Only 2 of these contained trees considered pure representatives of both species: Kaibab Trail (A-6) and Lofgreen (U-32). In addition to the 1- and 2-needled pinyons at these locations, there were also intermediate trees representing a wide range of variation, suggesting that these stands are active hybrid swarms. The other 32 populations were predominantly 1- or 2-needled but with an admixture of the other type.

The mean cone width of 17 mixed populations falls almost exactly midway between the means of pure populations of both species. The smallest cones of mixed populations are larger than those of pure *P. edulis,* but the largest mixed population cones exceed in size those of *P. monophylla (Tables 5—7)*.

Data from the two populations in which both species occur with intermediates are given below.

1. The hybrid swarm in the Great Basin (U-32):

The conifer flora of this area was recently described by LANNER (1971). Lofgreen is in the Great Basin, but the abrupt scarp of the Wasatch Mts. lies only about 30 miles to the east.

The 1-needled trees have the highest and most variable resin canal number, and the 2-needled trees the least *(Fig. 2)*. Trees that are intermediate in frequency of monophylly are aso intermediate in resin canal number.

Mean cone width at Lofgreen was just above the maximum mean of pure *P. edulis* and below the minimum mean of pure *P. monophylla* from Great Basin collections *(Tables 5—7)*.

Coincidence of flowering date is a necessary condition for natural hybridization. During the first week of June 1969 trees of all morphological types were shedding pollen profusely, and had pollen-receptive female conelets. During the second week of June 1972 trees of all types were

Table 4. — Frequency of 1-needle fascicles and leaf resin canal number in mixed populations diagnosed as *P. edulis* × *P. monophylla*[1])[2])

Plot	Location	Percent 1-needle fascicles	Mean Number of Resin canals per leaf
A- 3	Mt. Trumbull	6.0	2.0
A- 4	Page	9.0	2.1
A- 5	Cape Royal	1.7	2.0
A- 6	Kaibab Trail	50.2	2.2
A-10	Prescott	91.1	3.1
A-11	Sierra Ancha	85.1	2.9
A-13	Clifton	20.4	2.2
A-25	Apache Pass	58.1	2.4
A-26	Keating Canyon	76.1	2.1
N- 3	Pioche	97.8	4.2
NM- 1	Florida Mts.	93.1	6.2
U- 3	Mt. Logan	95.4	5.9
U- 4	Blacksmith Fork	89.9	4.1
U- 5	Porcupine Dam	66.3	3.6
U- 6	Eureka	88.5	—
U- 7	Oak City	95.3	3.7
U- 8	Frisco	95.7	6.0
U- 9	Wah Wah Mts.	80.6	7.7
U-10	Smith Mesa	78.1	2.2
U-11	Zion Canyon	85.8	—
U-12	Richfield	1.3	2.0
U-13	Cove Canyon	5.5	3.0
U-15	Cedar City	15.6	2.3
U-16	Crawford Mts.	15.8	2.7
U-21	Willow Creek	2.4	2.1
U-25	Mt Carmel Junction	7.2	2.0
U-26	Sevenmile Canyon	7.2	—
U-27	Orange Cliffs	3.0	2.0
U-28	Capitol Reef	3.9	2.0
U-29	Canyonlands	4.4	—
U-32	Lofgreen	55.2	2.7
U-33	White Canyon	4.9	2.1
U-39	Red Canyon	2.8	2.0
U-41	Confusion Mts.	90.5	4.2

[1]) Detailed plot data will gladly be furnished by the author upon request.
[2]) A = Arizona, N = Nevada, NM = New Mexico, U = Utah.

Table 5. — Width of seed cones from *P. monophylla* populations, in order of increasing size

Plot	No. cones	Millimeters	
		Range	Mean
A-12	4	44—65	54.5
C- 4	11	39—80	58.5
Mb- 2	7	53—72	58.7
C- 2	10	45—67	59.1
A-24	20	49—79	62.2
A-23	20	56—79	65.9
U- 2	10	61—78	68.8
U-43	14	64—79	71.2
U-24	5	65—78	72.6
A- 2	2	73—75	74.0
	103	39—80	$\bar{x}$ = 64.6

Table 6. — Width of seed cones from *P. edulis* populations, in order of increasing size

Plot	No. cones	Millimeters Range	Mean
Co- 7	5	20—38	27.0
A-27	6	31—44	35.8
Co- 6	16	34—55	39.4
NM- 6	16	30—49	40.0
A-20	18	34—48	40.8
NM- 2	22	28—57	40.8
NM- 5	17	35—53	42.1
NM- 3	16	32—63	42.9
U-38	3	37—51	46.0
Co- 5	15	36—60	48.5
U-37	10	35—63	51.4
U-14	10	41—68	54.9
	154	20—68	$\bar{x}$ = 42.5

Table 7. — Width of seed cones from mixed populations diagnosed as *P. edulis* × *P. monophylla*, in order of increasing size

Plot	No. cones	Millimeters Range	Mean
A-10	5	30—46	40.2
U-27	4	34—49	41.2
U-13	9	40—62	43.3
U-16	14	34—64	46.7
A-25	12	37—62	48.3
U-15	9	37—60	48.3
A- 6	3	40—57	48.7
A-26	20	36—63	49.1
NM- 1	46	37—66	51.3
U-12	14	33—73	53.5
U- 6	9	48—71	55.2
A-13	50	40—74	55.9
U- 9	9	44—66	56.9
U-32	31	39—79	57.6
U- 8	16	45—69	60.0
U- 7	9	64—80	71.5
A-11	5	71—87	76.2
	265	30—87	$\bar{x}$ = 53.2

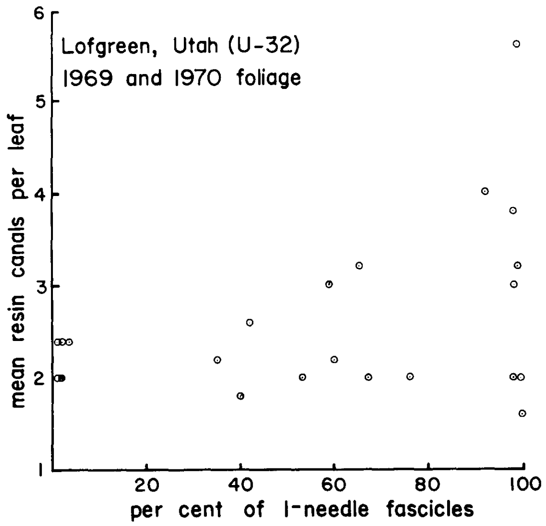

Fig. 2. — Relationship between frequency of monophylly and leaf resin canal number in trees from a hybrid swarm in central Utah.

on the verge of anthesis. Trees of both species have approximately equal growth rates and are intermixed randomly with regard to elevation, position on slope, and slope exposure. The only associated tree species is Utah juniper, and the major woody ground cover is of big sagebrush and prickly pear.

2. The hybrid swarm in the Grand Canyon (A-6):

A specimen with monophyllous needles attributed to Bright Angel Canyon was found in the herbarium of Grand Canyon National Park.

Therefore a descent was made during the first week of June 1970 down the North Kaibab Trail, from the Kaibab Plateau (about 8500 ft.) to Roaring Spring (about 5100 ft.). Trees from the plateau top to 6200 ft. were all classified as pure *P. edulis*. At 5600 ft. was pure *P. monophylla*, and intermediate trees. From 5500 ft. to 5100 ft. only pure *P. monophylla* was found.

In 5 trees between 6700 and 6200 ft. resin canal number ranged from 1—2; and tree means from 1.95—2.00. In 7 trees from lower elevations (5600—5100 ft.) the range in resin canal number was 1—6, and tree means varied from 1.90—3.60.

At Imperial Point (8800 ft.), male cones were just emerging from their covering scales and were still green. At 63000—6200 ft., pollen shedding was incipient or already in progress. From 5600 ft. down to 5200 ft. pollen had already shed and female conelets were closed.

Anomalous populations of P. monophylla

Two populations have been classified as *P. monophylla* despite high frequencies of 2-needled fascicles. Data will be presented here but justification will be deferred to the Discussion below.

1. Trees of the New York Mountains (C-2):

This population, according to an earlier report, consists of both *P. monophylla* and "a two-needled Piñon that does not seem to be different from *Pinus edulis* of Arizona (Wolf 1938: 45)." There is indeed a large component of 2-needle fascicles. One tree had 99 percent of 2-needle fascicles in foliage of 1967 and 1968, with the remaining needles in fascicles of 3. Another had 39 percent and 71 percent of 2-needle fascicles. But in other respects these trees differ greatly from *P. edulis*. For example, these trees, and all others sampled had resin canal numbers far in excess of that normally found in *P. edulis* (*Table 3*). Their needle length, cone size (*Table 5*), and seed coat thickness also were typical of *P. monophylla*. Of the 24 trees studied in detail, 16 qualified as pure *P. monophylla* on the basis of needle number. Three of these were 100 percent 1-needled.

2. Trees of the Grouse Creek Mountains (U-43):

There are extensive stands of *P. monophylla* in the Grouse Creek Mts., including the population at Rocky Pass (U-2). A tree at the southern end of the range had only 19 percent of its 1971 foliage in monophyllous fascicles: 81 percent of its fascicles were 2-needled. It had a mean resin canal number of 7.2 (range: 5—11). To ascertain the frequency of 2-needled trees in the stand, 114 trees were examined in transects radiating from this tree. Twenty-five fascicles were tallied per tree. Most of the samples entirely lacked 2-needle fascicles (*Table 8*). Many other trees were examined, and finally plot U-43 was established several miles further north. Moderate numbers of 2-needle fascicles were found in the plot and elsewhere in the vicinity, despite the close promixity to Rocky Pass (U-2) where few 2-needle fascicles were found (*Table 2*).

Pinyon pines of central and southern Arizona

Because Little recently created the variety *P. edulis* var. *fallax* for the 1-needled pines of central and southern Arizona, populations containing these trees were given close attention. Several previously unmapped stands were found, and the range of both 1- and 2-needled pinyons was ex-

Table 8. — Frequency of 2-needle fascicles in an anomalous *P. monophylla* stand in the Grouse Creek Mts., Utah (U-43)

Number of 2-needle fascicles per 25 fascicles	Number of trees
24	1
9	1
4	2
3	4
2	10
1	12
0	84

tended into the Chiricahua Mts. of southeastern Arizona *(Fig. 1)*[6]). According to LITTLE (1968: 335) "*P. monophylla* is known in Arizona only from the northwest corner", and therefore, his *P. edulis* var. *fallax* includes 1-needled pines from the Grand Canyon southeastwards to the Florida Mts. of New Mexico (NM-1). Eight of the "*fallax* areas" mentioned by LITTLE were visited (Grand Canyon [A-6], Oak Creek Canyon [A-8], Prescott [A-10], Sierra Ancha Experimental Forest [A-11], Apache Mts. [A-12], Pinaleño Mts. [apparently Crazy Horse Pass, A-24], north of Clifton [A-13], and Florida Mts. [NM-1]). One-needle fascicles were common to all of these locations except Oak Creek Canyon, which according to the criteria of this study, was classified as *P. edulis (Table 3)*. It therefore seems likely that the other seven populations coincided closely to LITTLE's sample areas. Four additional populations were sampled that might be expected to show characteristics of *P. edulis* var. *fallax:* Fort Bowie (A-20), Gila Mts. (A-23), Apache Pass (A-25), and Keating Canyon (A-26).

These populations were found to segregate into all three categories of *P. edulis*, *P. monophylla*, and mixed populations. Monophylly ranged from near-absence (A-8, A-20) to almost complete (A-23, A-24) on a populational basis *(Tables 2—4)*. One of these populations (Kaibab Trail, A-6) had trees of all three categories, thus qualifying as a hybrid swarm. Stands at Apache Pass (A-25) and Keating Canyon (A-26) had trees that were purely 1-needled and trees that were predominantly 2-needled *(Fig. 3)*. The population near Clifton (A-13) contained purely 2-needled trees and trees that were predominantly 1-needled *(Fig. 3)*.

Resin canal number varied widely, and the mean stand values were strongly correlated with the frequency of monophylly *(Fig. 3)*.

Cone width averaged 40.8 mm in stand A-8, classified as *P. edulis;* 52.8 mm in 7 mixed stands (A-6, A-10, A-11, A-13, A-25, A-26, NM-1); and 60.9 mm in 3 stands of *P. monophylla* (A-12, A- 23, A-24). Thus in the mixed stands south of the Mogollon Rim, as in those of the entire area encompassed in this study, average cone size was intermediate between that of *P. edulis* and *P. monophylla*.

Single-needled pinyons also occur in the Mule Mts. of southwest New Mexico (personal communication, R. S. PETERSON) and the Peloncillo Mts. of southeast Arizona (personal communication, S. BINGHAM). These locations are indicated in *Fig. 1*.

Discussion and Conclusions

The data on monophylly indicate that natural hybridization between *P. edulis* and *P. monophylla* is a widespread phenomenon. The rarity of monophylly elsewhere in *Pinus*, its occurrence in F_1 progeny of the controlled cross *P. monophylla* × *P. edulis*, and the abundance of intermediate forms in areas where both species are present leave little room for an alternative explanation.

The correlated shift of resin canal number and cone size in many of the plots for which data are available; and the coincidence of flowering phenology in hybrid swarms at Lofgreen and Kaibab Trail give further support to this interpretation. In addition, no areas have yet been found where both species are sympatric in the absence of intermediate forms.

It is not surprising that these two closely related species should hybridize spontaneously. Many analogous situations can be found in the genus *Pinus*, and the many similarities between the pinyon pines have caused them to be regarded by some taxonomists as varieties of a single species (SHAW

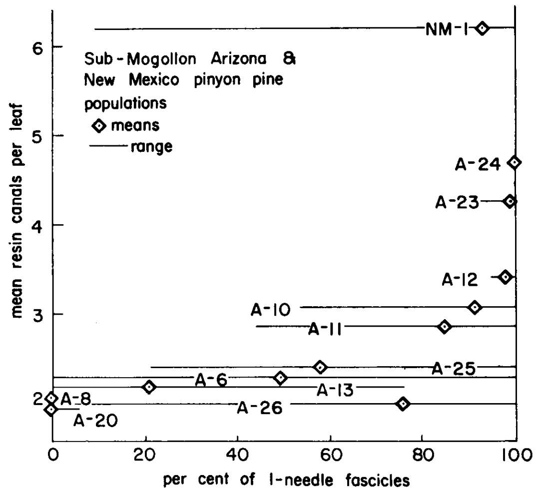

Fig. 3. — Relationship between frequency of monophylly and leaf resin canal number in pinyon pine populations from Arizona and New Mexico south of the Colorado Plateau.

1914). Perhaps what is most noteworthy is the geographic distribution of the populations in which hybridization has occurred. The mixed stands are found in 3 areas: the interface of the hydrographic Great Basin with the Utah Plateaus and Wasatch Mountains; the drainage of the Colorado River; and the complex of mountain ranges lying south of the Mogollon Rim of the Colorado Plateau *(Fig. 4)*.

The Great Basin Interface Zone

The eastern edge of the Great Basin roughly forms the boundary between *P. monophylla* and *P. edulis*. This is the interface that past reports have suggested as a hybridization zone.

The northernmost populations (U-3, U-4, U-5, U-16) were recently described by LANNER and HUTCHISON (1972). The Crawford Mts. (U-16) stand is *P. edulis* heavily introgressed by *P. monophylla,* while the other 3 stands are *P. monophylla* introgressed by *P. edulis*. Because these stands are disjunct from pure populations of both species, LANNER and HUTCHISON (1972) considered them relicts along migration routes of these species. The other mixed populations of this zone are in mountains close to the eastern edge of the great Basin (U-32, U-6, U-7, U-12, U-13, U-8, U-9, U-15, U-39, N-3). The hybrid swarm at Lofgreen (U-32) has already been described. All of the other stands are *P. monophylla* introgressed by *P. edulis,* except for 4 populations, where the reverse has occurred (U-12, U-13, U-15, U-39).

[6]) According to MARTÍNEZ (1948), *P. edulis* was collected by MEARNS in the Sierra de San José, Sonora, Mexico. Examination of the specimen, however, showed it to be *P. cembroides* ZUCC., as labelled by the collector.

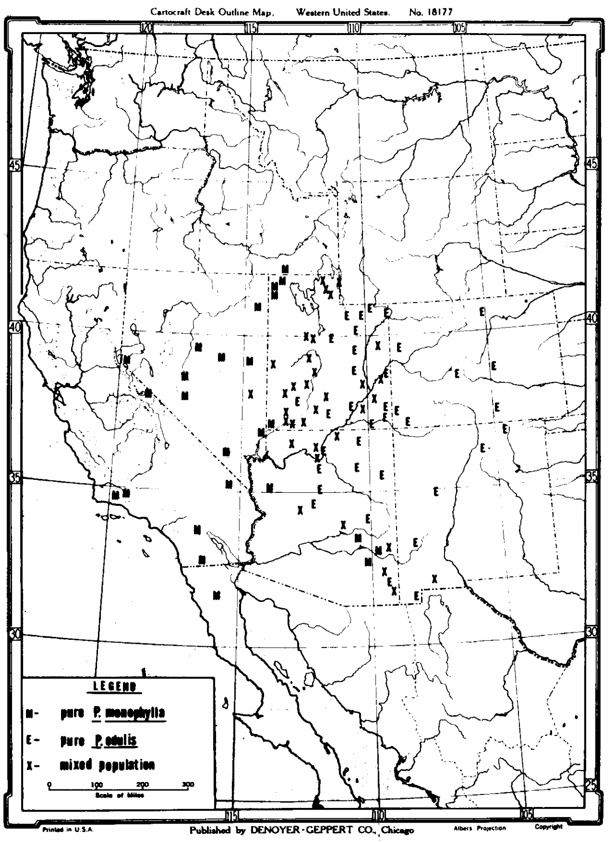

Fig. 4. — Classification of sample plots, showing geographic distribution of hybridized populations and parent species. © by DENOYER-GEPPERT COMPANY, CHICAGO. (Used by permission)

Gene flow from *P. edulis* into *P. monophylla* could be brought about by east-west pollen transport or by presence of *P. edulis* in the Great Basin. During the pollination period (June), winds aloft in this area are frequently from the southwest and very seldom easterly (personal communication, E. A. RICHARDSON, Utah State Climatologist), so large-scale dispersion of *P. edulis* pollen into the Great Basin is unlikely. It seems more probable that *P. edulis* was formerly distributed on some of the more easterly of the Great Basin mountain ranges, as it still is at Lofgreen.

The Great Salt Lake is an effective barrier to intermingling of pinyon pine species, but the mountains bordering its northern shore have been suggested as a past connection between the Wasatch Mts. and interior ranges of the northern Great Basin (LANNER and HUTCHINSON 1972).

The Anomalous Singleleaf Pinyon Populations

Has gene flow also proceeded westwards from *P. edulis* populations into stands of the New York and Grouse Creek Mts.? This would not be expected on the basis of prevailing wind direction. Nor is *P. edulis* known to have occurred closer than 90 miles to either of these locations. The morphological evidence is ambiguous because of the high frequency of 2-needle fascicles in occasional trees. However in both stands, the predominantly 2-needled trees had the very high resin canal numbers typical of 1-needled neighbors. Is there another explanation than gene flow from *P. edulis* to explain the occurrence of 2-needle fascicles in *P. monophylla?* I suggest as an alternative explanation, that the heavily 2-needled trees are back-mutants, and that less extreme trees are crosses between a back-mutant and the wild-type *P. monophylla*. The effect of the reverse mutation is to nullify the needle suppression mechanism that has differentiated *P. monophylla* from its 2-needled ancestor.

The low frequency of 2-needle fascicles at most other *P. monophylla* locations can be explained in either of two ways. First, the trees bearing them may have resulted from crossing between rare back-mutants and standard *P. monophylla* in past years.

Or the occasional 2-needle fascicle in a *P. monophylla* tree may result from a developmental "accident" — a failure of the needle suppression mechanism to be triggered during the critical ontogenetic phase of the fascicle.[7] This explanation appears to have some heuristic value in explaining low frequencies of 2-needle fascicles. It would explain the occurrence of rare 2-needle fascicles at west coast locations several hundred miles from the nearest *P. edulis* and on the opposite side of the Mohave Desert. I suggest that a low frequency of 2-needle fascicles can appear in any *P. monophylla* merely as a result of random developmental accidents during fascicle ontogeny. These fascicles do not indicate hybridization with *P. edulis,* and are not evidence of east-west gene flow.

Mixed Stands of the Colorado Drainage

Mixed populations of the Colorado River drainage tend to be located very close to the Colorado River or its major tributaries *(Fig. 1).*

The stands at Smith Mesa (U-10) and Zion Canyon (U-11) are predominantly *P. monophylla,* but both contain trees that are over 50 percent 2-needled. Extensive stands of *P. edulis* grow close by and it is probable that more intensive sampling in this area would disclose the presence of a hybrid swarm.

All of the other mixed stands of the Colorado River drainage are *P. edulis* introgressed by *P. monophylla,* except for the hybrid swarm on the North Kaibab Trail (A-6). Pollen of *P. monophylla* may have been available in the past from now-extinct stands that inhabited sites within the complex canyon system of the Colorado River. Such a situation still obtains within the Grand Canyon, and careful exploration of the canyon may disclose other *P. monophylla* stands at elevations of 5000—5500 ft.

No resin canal data are available for several of the mixed stands of the Colorado drainage. In several other stands resin canal number shows no marked departure from that of pure *P. edulis.* It is felt, however, that the frequency of 1-needle fascicles is too high to be accounted for without introgression of genes from *P. monophylla,* and it is worth noting that stands further east in Colorado (further from sources of *P. monophylla)* show progressively lower frequencies of monophylly. Gene flow would be facilitated by the dispersion of wind-borne pollen from both the Great Basin and former stands of *P. monophylla* in the Colorado River drainage. In June, winds aloft are predominantly from the southwest quadrant at Las Vegas, Nevada and Winslow, Arizona (personal communication, E. A. RICHARDSON, Utah State Climatologist). Prevailing winds from these directions would lead to the postulated pattern of pollen transport.

Mixed Stands South of the Mogollon Rim

The physiography of central Arizona is strikingly analogous to that of Utah. In both cases high plateaus drained

[7]) Unpublished data indicate that such an effect can be brought about by the oviposition activities of an as yet undescribed gall midge.

by the Colorado River, and forested with *P. edulis*, are bounded by basin-and-range country forested with *P. monophylla*. In both areas natural hybridization is evident at the border of the two zones. In central Arizona *P. monophylla* is now restricted to the complex of high mountains that roughly parallels the Mogollon Rim of the Colorado Plateau, but fossil evidence shows that during the Pleistocene it grew at elevations as low as 1800 ft. in southern Arizona (LANNER and VAN DEVENDER 1974; personal communication, T. R. VAN DEVENDER). Fossil locations are indicated in *Figure 1*.

The taxonomic status of Arizona's single-needled pines can now be examined. LITTLE (1968) explains the circumstances under which TIDESTROM named this entity *P. monophylla* var. *tenuis* TIDESTROM, but without Latin diagnosis. LITTLE considered it however to be a 1-needled form of *P. edulis*, and referred to it as such repeatedly (LITTLE 1950, 1951, 1962, 1965; CRITCHFIELD & LITTLE 1966). Elsewhere (LITTLE 1953) he reduced *P. monophylla* var. *tenuis* TIDESTROM to synonymy with *P. edulis* ENGELM. without mention of a 1-needled form. Earlier LITTLE (1949) published a map showing *P. edulis* in central Arizona, also without mention of a 1-needled form. The same procedure was followed later in his *Atlas* (LITTLE 1971). The map in MIROV's (1967) monograph is one of the very few published in over 3 decades showing *P. monophylla* extending across central Arizona, though foresters in that area generally have called these trees *P. monophylla* (LITTLE 1968). In 1968 LITTLE formally placed these 1-needled pines in the new variety *P. edulis* ENGELM. var. *fallax* LITTLE.

I prefer to retain these trees under the species *P. monophylla* for several reasons. First, as mentioned above, singleleaf pinyon must be viewed as a mutant form of an ancestral *P. edulis*. The monophylly mutation is unknown elsewhere in the genus and must be considered a rare event. It is simpler to postulate a single occurrence of this mutation rather than multiple occurrences, unless compelling evidence demands otherwise. Thus all single-needle pinyon pines are viewed as members of a single line which has undergone speciation. LITTLE (1968: 335) however feels that monophylly has arisen independently in *P. monophylla* and *P. edulis* var. *fallax*.

The geographic evidence favors the single-origin hypothesis. Single-needled trees extend from southwest New Mexico and southeast Arizona to northwest Arizona; and thence into the Great Basin and the Mohave Desert area. Fossil evidence shows that single-needled trees formerly occupied the low mountains of southern Arizona during the Pleistocene *(Fig. 1)*. There is no major discontinuity between *"P. edulis* var. *fallax"* and *P. monophylla* of the Great Basin or Mohave Desert border. Thus the single-needled pines of the southwest form a single population system *(Fig. 4)*.

Finally, the pattern of morphological variation demonstrates conclusively that *"P. edulis* var. *fallax"* is not a distinct entity, but rather an assortment of biotypes that comprise a narrow portion of the range of variability of hybridized and introgressed populations. LITTLE (1968: 334) says of *P. edulis*: "Plants of the new, 1-needle variety bear 2-needle fascicles rarely. Plants of the typical, 2-needle variety produce 3-needle fascicles rarely but not 1-needle fascicles." Yet the populations containing 1-needled trees show the complete range of variation from purely 2-needled to purely 1-needled trees *(Figure 3)*. Even on the Sierra Ancha Experimental Forest (A-11), the type locality of var. *fallax*, the range of variation is much broader than LITTLE's description.

The same is true of leaf characters. According to LITTLE (1968: 334), *P. edulis* var. *fallax* has 2—4 resin canals. But 3 of these 1-needled populations (A-23, A-24, NM-1) have *mean* resin canal numbers higher than the *maximum* reported by LITTLE, and at A-24 and NM-1 the range is 2—10 *(Figure 3)*. These values do not suggest a closer relationship to *P. edulis* than to *P. monophylla*, but rather the opposite.

According to LITTLE's counts (1968: 334) *P. monophylla* has 20—36 rows of stomates while the "new variety" has 11—15 rows. Data presented in more detail elsewhere (LANNER and VAN DEVENDER 1974) show a range of 11—23 for several of the central Arizona populations (A-12, A-23, A-24), 11—18 in the Hualapai Mts. (A-2) 15—22 for a California source (C-3), and 13—20 for a Baja California source (Mb-2). In the Grouse Creek Mts. (U-43) there were 25—44 stomatal rows. So this feature is variable, and while the "new variety" indeed differs sharply from trees of the northern Great Basin, it differs little from unquestioned *P. monophylla* further south.

Other data could be cited that differ materially from those used by LITTLE to define the "new variety". A point of agreement however can be found regarding needle size. Single-needles from central and southern Arizona are shorter and thinner than those from most Great Basin and Mohave Desert sources. Undoubtedly detailed study of *P. monophylla* would disclose geographic variation in many other characters across its broad range, either clinal or discontinuous.

In conclusion, *"P. edulis* var. *fallax"* is by no means a stable entity. Instead, the pattern of variation is similar to that along the Great Basin interface, where hybridization is rampant. The purely 1-needled populations (A-12, A-23, and A-24) can be considered *P. monophylla*. The populations NM-1, A-10, A-11, A-25, and A-26 are *P. monophylla* hybridized by *P. edulis*. At Clifton (A-13) the stand is made up of *P. edulis* hybridized by *P. monophylla*. Further search in these latter 2 categories may disclose hybrid swarms like the Kaibab Trail stand (A-6).

This study has differed from most forest-tree investigations in having been facilitated by a unique genetic marker. The existence of this marker., and the fairly detailed data available on southwestern paleobotany make it possible to trace the evolution of *P. edulis* and *P. monophylla* with some confidence. This task is now underway.

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Summary

Natural hybridization between *P. edulis* and *P. monophylla* has been suspected by several investigators. In this study the frequency of monophyllous fascicles was used as the major character in detecting evidence of hybridization, with additional evidence provided by other morphological features. It is concluded that hybridization has occurred on a grand geographic scale in three zones: the eastern edge of the Great Basin, the canyon country of the Colorado River, and the mountains south of the Colorado Plateau. Populations containing the 1-needled trees of the mountains south of the Colorado Plateau, recently described as *P. edulis* ENGELM. var. *fallax* LITTLE, are shown to exhibit the same pattern of variation as populations in more northerly areas where hybridization has occurred. It is therefore suggested that these trees be retained under the name *P. monophylla*.

Key words: Natural hybridization, introgression, geobotany, paleobotany, evolution.

Zusammenfassung

Natürliche Bastardierung zwischen *Pinus edulis* und *P. monophylla* wurde früher schon vermutet. In der vorliegenden Publikation benutzte man die Häufigkeit einnadliger Kurztriebe als Hauptmerkmal, um ein Vorhandensein von Hybridisation nachzuweisen. Es ließ sich der Schluß ziehen, daß sich diese Hybridisation großräumig in 3 Zonen ereignet hat: Ostteil des Great Basin, im Canyon-Gebiet des Colorado-Flusses und in den Gebirgen südlich des Colorado-Plateaus. Die einnadelige Bäume enthaltenden Populationen der letztgenannten Zone, die kürzlich als *P. edulis* var. *fallax* beschrieben worden waren, hatten dasselbe Variationsmuster wie diejenigen in nördlicheren Gebieten, wo Hybridisierung aufgetreten ist. Es wird deshalb vorgeschlagen, daß auch diese Bäume den Namen *Pinus monophylla* behalten sollten.

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Resistance of Ponderosa Pine to Dwarf Mistletoe

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Improvement of genetic resistance is receiving increasing attention as a means of controlling forest diseases (GERHOLD *et al.* 1966, U. S. Forest Serv. 1972, BINGHAM, HOFF, and MCDONALD 1971). The procedures are applicable especially to introduced diseases where tree hosts lack the resistance that naturally evolves from long association of host and parasite and to native diseases where intensified silviculture has greatly aggravated damage from organisms that are relatively innocuous in the natural forest. A less common situation in which improvement of resistance is appropriate is the native disease in its natural environment where, for one reason or another, a high level of resistance has failed to develop. The dwarf mistletoes (*Arceuthobium* spp.) are good examples of this condition.

Since dwarf mistletoes are currently the most destructive pathogens in the coniferous forests of western North America (CHILDS and SHEA 1967) it may appear surprising that no effort is being made to improve resistance to these parasites. This situation results from the rather common conviction that damage can be effectively controlled by silvicultural methods. This belief disregards the facts that: 1) the availability of resistant stock could greatly improve the silvicultural control program and, 2) investments that would bear much of the cost of improving disease resistance are already being made in improving other characteristics of some of the major susceptible species. Indifference to the possibilities of genetic control in forest practice has greatly limited acquisition of knowledge of the basic biological resources available for genetic control. Every fragment of information to be had would therefore seem potentially useful. This report concerns the availability of genetic resistance in ponderosa pine (*Pinus ponderosa* LAWS.) to western dwarf mistletoe (*Arceuthobium campylopodum* ENGEL.).

Problems in identifying resistant trees

The first step to improve disease resistance usually involves a search for sources of genes for resistance. Only part of the pine forest is available for this purpose because

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